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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

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Fishery Bulletin

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STOMACH CONTENTS OF SILVER HAKE, *MERLUCCIUS BILINEARIS*, AND ATLANTIC COD, *GADUS MORHUA*, AND ESTIMATION OF THEIR DAILY RATIONS

E. G. DURBIN,[1] A. G. DURBIN,[1] R. W. LANGTON,[2] AND R. E. BOWMAN[3]

ABSTRACT

The model of Elliott and Persson was used to estimate the daily ration of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, collected in the western North Atlantic between Cape Hatteras and Nova Scotia during the years 1973-76. The model required field measurements of the weight of food in the stomachs during consecutive 3-h periods over 24 h, and laboratory estimates of the exponential gastric evacuation rate. The silver hake and Atlantic cod were each grouped into two size classes for analysis (≤20 cm and >20 cm, and ≤30 cm and >30 cm, respectively). Upper and lower daily ration estimates were 3.2 and 2.9% body weight (BW) per day for hake ≤20 cm, 2.2 and 0.8% BW per day for hake >20 cm, and 1.5 and 0.9% BW per day for cod >30 cm. There were insufficient small cod to estimate daily ration. These ration estimates are intermediate between two previous estimates for silver hake and Atlantic cod on Georges Bank obtained by different methods.

With the increasing interest in multispecies management and total ecosystem management, it is essential to understand the role of fish predators within the ecosystem. As a part of this, it is necessary to determine the feeding habits and the daily ration of the major species. Here we estimate the daily ration of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, in the northwest Atlantic, based on stomach samples collected by the Northeast Fisheries Center, National Marine Fisheries Service. The model of Elliott and Persson (1978) was used to investigate diel feeding periodicity and to estimate the daily ration, based on field measurements of stomach contents, and laboratory estimates of the exponential evacuation rate R.

METHODS

Method of Estimating Daily Food Consumption

Most recent studies have concluded that gastric evacuation is best described by a curvilinear function such as an exponential curve (Tyler 1970; Brett and Higgs 1970; Elliott 1972; Kiørboe 1978; Persson 1979; but see Jobling 1981). In an evaluation of different models to estimate daily ration in fishes, Elliott and Persson (1978) demonstrated that their model, which assumes exponential evacuation, provided accurate estimates of ingestion, whereas models which assumed a constant (linear) gastric evacuation rate (Bajkov 1935 and derivations thereof) significantly underestimated ingestion. Since recent comments support the validity of the exponential model for the field estimation of daily ration on the basis of stomach contents (Cochran 1979; Elliott 1979; Eggers 1979), this approach has been adopted for the present analysis.

In the Elliott and Persson model, the consumption of food (C_t) by a fish over the time interval t_0 to t_t is calculated from the amount of food in the stomach at time t_0 (S_0), the amount in the stomach at time t_t (S_t), and the instantaneous evacuation rate R:

$$C_t = \frac{(S_t - S_0 e^{-Rt})\, Rt}{1 - e^{-Rt}}. \quad (1)$$

To apply the model, a sample of fish is collected from the field at intervals of t hours for at least 24 h, and the mean stomach content weight is used to estimate S_0 and S_t for each time interval. The estimates of C_t calculated for each time interval t are then summed to give the total daily ration.

The model assumes that the fish feed continuously, at a constant rate, during time interval t. The cumulative amount of food consumed (C_t) therefore increases linearly during time t. However, Elliott and Persson (1978) showed that even if feeding is not

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continuous, the estimates of C_t will not be seriously biased, provided that stomach samples are collected at intervals of 3 h or less.

The total daily ration can also be calculated in a single step from

$$C_t = 24\,R\,\bar{S} \qquad (2)$$

where $\bar{S}$ equals the mean stomach content weight over the 24-h period (Elliott and Persson 1978). However, in order to investigate diel feeding periodicity, it is necessary to calculate ingestion during time intervals <24 h, using Equation (1). For the present analysis the 24-h day was divided into eight consecutive 3-h time periods; data collected within each of these periods were arbitrarily assigned to the midpoint of that time period. Ingestion between that time and the midpoint of the next time interval was then calculated using Equation (1), where $t = 3$ h.

In the Elliott and Persson model, R is assumed to be exponential (i.e., a constant proportion of the stomach content is evacuated per unit time), and unaffected by fish size, food size, meal size, and the frequency of feeding. R is affected by food type, however, and increases with increasing temperature, usually following an exponential or power curve. Gastric evacuation is assumed to begin immediately after the food is ingested, without an appreciable time lag.

The most appropriate values of R to be used in this analysis were determined from a literature review (Appendix 1). The general relationship between R and temperature (t) is that $R = ae^{bt}$ (Elliott 1972), where a and b are constants. The slope (b) of this relationship appears to be fairly constant for different prey types and fish species ($\bar{b} = 0.115$, App. Table 1) but the intercept (a) may change significantly according to the type of food.

For several marine fishes that were fed small prey, the relationship between R and temperature (°C) was

$$R = 0.0406\,e^{0.111t} \qquad (3)$$

(App. Fig. 1). The data indicated that fish prey are digested more slowly than small prey types, however. This effect has not been clearly defined, but the maximum range in R that has been observed within a single fish species was in the Atlantic cod, where the exponential evacuation rate for fish flesh (based on our calculation of data from Bagge 1977) was about 10% of that for a crustacean prey, shrimp tails (Tyler 1970) (App. Fig. 1). A complicating factor is that the food particle sizes in those studies using fish as prey were much larger than in studies using other prey types, and the effect of large particle size on the evacuation rate is poorly known. Thus we are not presently able to determine whether the reduced evacuation rates observed for fish prey are principally due to the prey type (fish flesh) or to the comparatively large particle sizes used in these studies. A further problem is that we lack information on digestive rates for many important prey species of marine fishes.

Because of these limitations to our knowledge of the rates at which different prey species are evacuated, the stomach contents of the Atlantic cod and silver hake have been grouped into two categories in the present study: "fish prey" and "all other prey." Most of the "other prey" were small organisms, and we used Equation (3) to estimate R for these prey. Because of the uncertainty concerning the value of a for fish prey, we made two estimates of R for this food type: first, where a in Equation (3) = 0.0406, and second where a was 10% of this value, i.e., a = 0.00406. These estimates should represent upper and lower limits to the true value of R for fish prey. The temperature for which R was calculated was the mean temperature at which each fish species and size class was collected (see Tables 1, 6, 7).

Description of the Data Set

The survey area from which stomach samples were taken extends from the offshore waters of Cape Hatteras to western Nova Scotia, and is divided into five geographic regions (Fig. 1). Stomach content data gathered during spring and fall cruises (Table 1) during the years 1973-76 were analyzed. Details of the sampling procedure and methods of stomach content analysis are given in Langton et al. (1980). Sampling continued throughout the 24-h day and was designed to provide broad coverage over a wide geographic area rather than intensive surveys within small regions. In order to define the food web, 100 stomachs (50 young-of-the-year and 50 adult fish) were to be collected per geographic region per cruise from each of 17 selected fish species. At each station no more than 10 stomachs per species were to be sampled. The same species was not to be sampled from consecutive stations unless it appeared that, because of low abundance, the desired number of fish could not be collected using the normal sampling scheme. In this case the fish were collected as needed to fill the quota for the geographic area. Young-of-the-year fish were preserved whole in 10% Formalin,[4] after slitting the gut cavity to ensure quick penetra-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

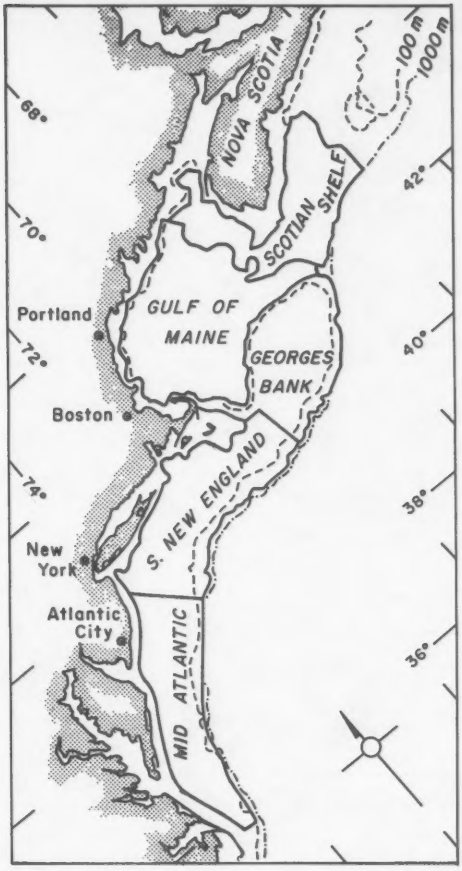


FIGURE 1.—Five geographic areas of the northwest Atlantic composing the sampling area for fish food studies.

tion by the preservative. With the larger fish the length, sex, and maturity were determined at sea, and the stomach was then removed, individually labeled, and preserved in 10% Formalin for later analysis. Fish showing signs of regurgitation (everted stomach, food present in mouth or esophagus) were not included in the samples. In the laboratory the stomach contents were identified to the lowest possible taxon and weighed (wet weight). For the present study, the weight of sand and gravel were subtracted from the total stomach content weight, and stomachs that contained recognizable food in amounts too small to be weighed (<0.01 g) were considered empty.

The weight of each fish was calculated from its total length and length-weight relationships (Wilk et al. 1978) where

$$\text{Wet wt (g)} = 0.3555 \times 10^{-5} \text{ length (mm)}^{3.1109} \quad \text{(silver hake)}$$

$$\text{Wet wt (g)} = 0.6031 \times 10^{-5} \text{ length (mm)}^{3.0979} \quad \text{(Atlantic cod).}$$

Combining all cruises, 1,159 silver hake were collected during the spring, and 1,555 during the fall; the number of fish sampled per tow averaged 8.0 and 8.6, respectively (Table 1). Silver hake were collected almost exclusively in the southern three geographic regions (Middle Atlantic, Southern New England, and Georges Bank), where a total of 2,625 fish were taken in 304 tows. Mean temperatures during spring cruises were several degrees colder than during the fall; however, the mean depth at which the fish were collected was not greatly different during the two seasons (Table 1).

In all cruises combined, 775 Atlantic cod were sampled during spring, and 922 during fall; the average number of fish sampled per tow (5.0 and 4.5, respectively) was lower than for silver hake. Atlantic cod were collected mainly from the northern three geographic regions (Georges Bank, Gulf of Maine, and Western Nova Scotia), where a total of 1,661 fish were sampled from 351 tows. The temperatures at which cod were collected in the spring were colder than those at which they were taken in the fall. Because of the more northerly distribution of the cod, they were taken from colder water temperatures than the silver hake (Table 1). The depths at which hake and cod were taken during the spring were similar (Table 1). However, during fall, the cod were found at somewhat greater depths than hake.

Because of the considerable size range of each species (Fig. 2), and changes in food habits which occurred with increasing size (discussed below), the silver hake and Atlantic cod were divided into two size-classes for further analysis: ≤20 cm (small) and >20 cm (large) for hake, and ≤30 cm (small) and >30cm (large) for cod. Mean lengths and weights of each size class during spring and fall are presented in Table 2.

For the present study, the data from the four spring cruises were combined to provide a composite picture of diel changes in stomach contents of each species over the entire study area. Data from the four fall cruises were similarly combined. Possible differences in diel feeding patterns or feeding rate that may have existed in different regions or years are not

TABLE 1.—Total number of tows from which silver hake and Atlantic cod were sampled, total number of fish sampled, mean number of fish sampled per tow, and mean temperature and depth of capture. Cruise dates were: (Spring) 3/3 to 15/5 1973; 12/3 to 4/5 1974; 4/3 to 12/5 1975; 4/3 to 8/5 1976; (Fall) 26/9 to 20/11 1973; 20/9 to 14/11 1974; 15/10 to 18/11 1975; 20/10 to 23/11 1976.

	Total no. of tows	Total no. of fish sampled	No. of fish per tow $\bar{x}$	Temperature of capture (°C) $\bar{x} \pm$ 95% C.L.	Depth of capture (m) $\bar{x} \pm$ 95% C.L.
Silver hake					
Spring					
All fish	144	1,159	8.0	8.08 ± 0.17	88.4 ± 3.8
≤20 cm				7.63 ± 0.23	64.1 ± 3.7
>20 cm				8.45 ± 0.23	106.6 ± 5.7
Fall					
All fish	180	1,555	8.6	11.86 ± 0.10	82.6 ± 2.3
≤20 cm				11.94 ± 0.15	75.5 ± 3.2
>20 cm				11.76 ± 0.13	90.1 ± 3.3
Atlantic cod					
Spring					
All fish	155	775	5.0	5.76 ± 0.16	90.3 ± 2.9
≤30 cm				5.72 ± 0.48	89.6 ± 5.9
>30 cm				5.77 ± 0.17	90.4 ± 3.2
Fall					
All fish	204	922	4.5	9.15 ± 0.15	104.8 ± 3.1
≤30 cm				8.46 ± 0.30	87.1 ± 4.6
>30 cm				9.30 ± 0.17	108.6 ± 3.5

TABLE 2.—Mean length and estimated wet weight of silver hake and Atlantic cod.

		Total length (cm)			Wet weight (g)		
	n	$\bar{x} \pm$ 95% C.L.	Minimum	Maximum	$\bar{x} \pm$ 95% C.L.	Minimum	Maximum
Silver hake							
Overall	2,714	20.3 ± 0.5	3	64	125.8 ± 6.6	0.1	1,908
Spring	1,159	23.0 ± 0.7	3	64	156.0 ± 11.4	0.1	1,908
≤20 cm	496	10.2 ± 0.4	3	20	9.9 ± 1.0	0.1	51.2
>20 cm	663	32.6 ± 0.5	21	64	265.3 ± 15.4	59.6	1,908
Fall	1,555	18.3 ± 0.6	3	55	103.3 ± 7.5	0.1	1,191
≤20 cm	797	7.2 ± 0.2	3	20	4.1 ± 0.6	0.1	51.2
>20 cm	758	30.1 ± 0.4	21	55	207.7 ± 11.3	59.6	1,191
Atlantic cod							
Overall	1,697	53.2 ± 1.2	4	150	2,861 ± 170	0.6	41,649
Spring	775	54.5 ± 1.8	4	133	3,062 ± 259	0.6	28,693
≤30 cm	143	18.8 ± 1.3	4	30	104.5 ± 16.5	0.6	285
>30 cm	632	62.6 ± 1.5	31	133	3,732 ± 293	315	28,693
Fall	922	52.2 ± 1.5	5	150	2,692 ± 225	1.1	41,649
≤30 cm	161	17.9 ± 1.2	5	30	90.5 ± 13.6	1.1	285
>30 cm	761	59.5 ± 1.4	31	150	3,243 ± 256	315	41,649

considered; evaluation of such differences would require a separate study, with additional, more intensive field surveys designed to investigate these problems (see Pennington et al. (in press) for a discussion of the required sampling design).

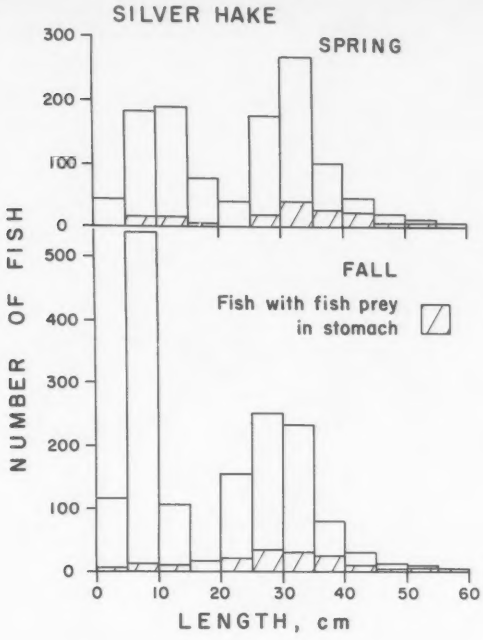
As stated above, for the analysis of diel changes in stomach contents and the calculation of daily ration, data from tows within each successive 3-h period of the day were grouped together and arbitrarily assigned to the midpoint of the time period. The number of tows taken during each period is shown for each species by season and size class in Tables 6 and 7. Large silver hake and large Atlantic cod were fairly evenly sampled throughout the day. Small hake were caught in larger numbers by night, however. Small cod were few, and generally the sample sizes for each time period were very small (<10 individuals).

In order to compare mean values from different subsets of the data, an F-test for the equality of variances was first performed. If the variances were not significantly different ($P < 0.05$), a Student's t-test was applied to test for the significance of the difference in the mean values of the two subsets. If the variances were unequal, Satterthwaite's approximation (Steel and Torrie 1960) was used to compute the degrees of freedom associated with the approximate t value, using a computer program which is available in the Statistical Analysis System (SAS 79) statistical package (SAS Institute, Inc.).

RESULTS

Stomach Contents

In both Atlantic cod and silver hake, the food habits and the mean amount of food in the stomachs changed with increasing fish length (Tables 3, 4). The



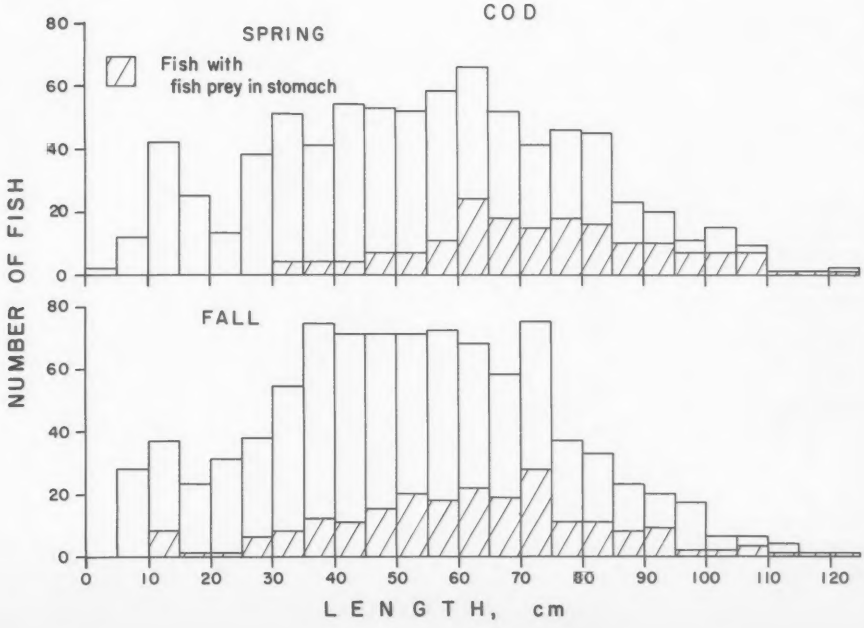


FIGURE 2.—Size-frequency distribution of silver hake and Atlantic cod collected during the spring and fall in the study area. The number of fish in each size class containing fish prey in their stomachs is also shown.

proportion of fish prey in the diet increased as the fish grew larger. This change in food habits was accompanied by an increase in the mean weight of stomach contents as a percent of body weight (Tables 3, 4). Thus, on the average, the stomachs of large fish contained more food, as a percent of body weight, than the stomachs of small fish (see especially the mean values for fish with nonempty stomachs, last three columns in Tables 3 and 4).

In silver hake, the "other prey" category was im-

TABLE 3.—Mean weight of stomach contents of silver hake, in 10 cm length classes, during spring and fall. BW = body weight.

Size class (cm)	Total no. of fish examined (No. of empty stomachs)	Mean stomach contents of all fish, including those with empty stomachs						Stomach contents, excluding fish with empty stomachs		
		Total wet wt per fish (g)	Fish prey wt per fish (g)	Other prey wt per fish (g)	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish
Spring										
1-10	283(79)	0.022	0.005	0.017	0.73	0.15	0.58	1.01	0.21	0.80
11-20	213(42)	0.19	0.024	0.16	0.86	0.14	0.72	1.08	0.18	0.90
21-30	264(95)	0.84	0.30	0.54	0.63	0.22	0.41	0.98	0.35	0.64
31-40	332(147)	3.15	2.19	0.95	1.00	0.67	0.33	1.79	1.20	0.59
41-50	53(18)	21.99	19.82	2.17	3.10	2.80	0.30	4.70	4.24	0.46
51-60	13(6)	24.54	24.51	0.027	2.29	2.29	0	4.26	4.25	0.00
61-70	1(1)	0	0	0	0	0	0	0	0	0
All Fish	1,159(388)	2.41	1.88 (78.0%)	0.53 (22.0%)	0.93	0.46 (49.2%)	0.47 (50.8%)	1.40	0.69 (49.3%)	0.71 (50.7%)
Fall										
1-10	697(144)	0.016	0.001	0.015	1.08	0.08	1.00	1.36	0.10	1.26
11-20	100(28)	0.17	0.046	0.12	0.92	0.19	0.73	1.28	0.27	1.01
21-30	448(218)	0.32	0.18	0.14	0.29	0.17	0.13	0.57	0.33	0.24
31-40	264(113)	2.66	2.25	0.41	0.83	0.68	0.15	1.45	1.19	0.27
41-50	38(22)	10.07	10.04	0.032	1.71	1.70	0.01	4.06	4.04	0.01
51-60	8(3)	15.84	15.80	0.047	1.59	1.58	0	2.54	2.53	0.01
61-70	0							0		
All fish	1.555(528)	0.89	0.76 (85.4%)	0.13 (14.6%)	0.82	0.26 (31.4%)	0.56 (68.6%)	1.24	0.39 (31.5%)	0.84 (67.7%)

TABLE 4.—Mean weight of stomach contents of Atlantic cod, in 10 cm length classes, during spring and fall. BW = body weight.

Size class (cm)	Total no. of fish examined (No. of empty stomachs)	Mean stomach contents of all fish, including those with empty stomachs						Stomach contents, excluding fish with empty stomachs		
		Total wet wt per fish (g)	Fish prey wt per fish (g)	Other prey wt per fish (g)	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish
Spring										
1-10	13(1)	0.0064	0	0.0064	0.59	0	0.59	0.64	0.00	0.64
11-20	71(11)	0.11	0	0.11	0.39	0	0.39	0.46	0.00	0.46
21-30	59(5)	1.15	0.0017	1.15	0.52	0	0.52	0.57	0.00	0.57
31-40	92(7)	2.63	0.28	2.35	0.57	0.07	0.50	0.61	0.07	0.54
41-50	107(6)	5.31	0.43	4.87	0.49	0.04	0.45	0.52	0.04	0.48
51-60	114(11)	13.12	0.87	12.25	0.66	0.04	0.62	0.73	0.05	0.69
61-70	110(5)	34.42	13.42	21.00	1.09	0.42	0.68	1.15	0.44	0.71
71-80	86(5)	45.52	25.38	20.14	0.90	0.50	0.40	0.96	0.53	0.43
81-90	66(1)	38.53	25.85	12.68	0.55	0.36	0.19	0.55	0.37	0.19
91-100	28(2)	99.02	58.21	40.82	0.99	0.59	0.40	1.06	0.63	0.43
101-110	23(3)	190.02	160.80	29.22	1.39	1.18	0.21	1.59	1.36	0.24
111-120	2(0)	27.30	12.70	14.60	0.13	0.06	0.07	0.13	0.06	0.07
121-130	3(0)	627.96	575.92	52.04	2.50	2.28	0.22	2.50	2.28	0.22
131-140	1(0)	658.00	658.00	0	2.29	2.29	0	2.29	2.29	0.00
All fish	775(57)	28.86	17.13 (59.4%)	11.73 (40.6%)	0.71	0.23 (32.6%)	0.48 (67.4%)	0.77	0.25 (32.5%)	0.51 (66.2%)
Fall										
1-10	35(10)	0.034	0.002	0.032	0.75	0.02	0.73	1.05	0.03	1.02
11-20	63(14)	0.095	0.008	0.087	0.28	0.04	0.24	0.36	0.05	0.31
21-30	63(9)	1.14	0.53	0.61	0.72	0.40	0.31	0.84	0.47	0.37
31-40	144(12)	2.15	0.44	1.72	0.42	0.08	0.34	0.46	0.09	0.37
41-50	149(8)	6.82	2.98	3.84	0.62	0.27	0.34	0.65	0.29	0.36
51-60	128(16)	11.96	6.75	5.22	0.64	0.37	0.27	0.73	0.42	0.31
61-70	129(14)	17.92	11.39	6.53	0.56	0.35	0.20	0.62	0.39	0.23
71-80	109(13)	23.39	16.79	6.60	0.48	0.34	0.14	0.55	0.39	0.16
81-90	49(7)	62.39	54.23	8.16	0.83	0.72	0.11	0.97	0.84	0.13
91-100	34(4)	113.95	63.65	50.30	1.08	0.61	0.46	1.22	0.69	0.53
101-110	11(3)	48.12	39.21	8.91	0.36	0.30	0.06	0.50	0.42	0.08
111-120	4(0)	399.86	96.17	303.70	2.36	0.56	1.80	2.36	0.56	1.80
121-130	3(0)	709.41	709.41	0	2.82	2.82	0	2.81	2.81	0.00
131-140	0							0		
141-150	1(0)	98.02	0	98.02	0.24	0	0.24	0.24	0.00	0.24
All fish	922(110)	20.70	13.52 (65.3%)	7.17 (34.6%)	0.59	0.30 (51.4%)	0.29 (48.6%)	0.67	0.35 (52.2%)	0.33 (49.3%)

portant in the diet up to a size of about 40 cm; hake >40 cm fed almost exclusively on fish. The mean weight of "fish prey" exceeded that of "other prey" in all silver hake size classes >30 cm during spring, and >20 cm during fall (Table 3).

In contrast to silver hake, Atlantic cod in all size classes fed on "other prey" to a significant degree. Fish prey was absent from the diet of cod ≤30 cm during the spring, but was observed in all size classes in the fall (Table 4). Fish prey constituted a significant portion of the diet in cod >60 cm during spring, and >30 cm during fall, but the mean weight of fish prey did not exceed that of other prey except in cod >70 cm (spring) or >50 cm (fall).

The total weight of food as a percentage of body weight was significantly greater ($P < 0.05$) in the hake than in the cod during both the spring and the fall (Table 5). During spring, hake contained significantly more fish prey (% BW) than cod, but the amount of "other" prey was not significantly different ($P < 0.05$) (Table 5). During the fall, the amount of fish prey was not significantly different, but hake contained significantly more "other" prey than cod.

The mean stomach content weight as a percentage of body weight of the large silver hake was significantly greater ($P < 0.05$) than the small silver hake during spring, while during the fall the stomach content weight of the small hake was greater. During both seasons, large hake contained significantly ($P < 0.05$) more fish prey than the small hake (Table 5); the large hake contained 66.2 and 77.3% fish prey as a percentage of body weight during spring and fall, respectively, and the small hake 18.7 and 8.5%, respectively.

Fish prey constituted 0 and 32.1% of the stomach contents of small Atlantic cod, and 37.4 and 55.1% of the stomach contents of large Atlantic cod during spring and fall, respectively. During spring, small cod contained a lower mean stomach content, as a percentage of body weight, than large cod (Table 5). This was due to the lack of fish prey in the diet of small cod, since the amount of food in the "other" category did not differ significantly between the two size classes. During fall, the mean stomach contents (total, fish and "other" prey) as a percentage of body weight did not differ ($P < 0.05$) between the two size classes of cod.

The mean weight of food in the stomachs of each group of fish did not exceed 1.0% BW (body weight), but the range of values observed in individual fish extended from 0 to 23.7% (Table 5). In general, the maximum observed values for the fish prey category were larger than those for the other prey category (especially in Atlantic cod). Among silver hake, the maximum values for large fish were greater than for small

TABLE 5.—Overall mean and 95% confidence limits, minimum and maximum values, and median stomach contents of the different categories of silver hake and Atlantic cod. BW = body weight.

		Stomach contents, all fish including those with empty stomachs					Stomach contents, excluding fish with empty stomachs		
		No. of fish	Mean ± 95% C.L. (% BW)	Min (% BW)	Max (% BW)	Median (% BW)	No. of fish	Mean ± 95% C.L. (% BW)	Median (% BW)
Silver hake									
≤20 cm									
Spring	Total food	496	0.785 ± 0.104	0	12.86	0.439	375	1.039 ± 0.127	0.741
	Fish prey	496	0.147 ± 0.083	0	12.86	0	375	0.195 ± 0.110	0
	Other prey	496	0.638 ± 0.071	0	4.55	0.374	375	0.844 ± 0.083	0.586
Fall	Total food	797	1.056 ± 0.094	0	10.37	0.583	625	1.346 ± 0.110	0.891
	Fish prey	797	0.090 ± 0.046	0	10.37	0	625	0.115 ± 0.058	0
	Other prey	797	0.966 ± 0.084	0	9.63	0.498	625	1.232 ± 0.098	0.866
>20 cm									
Spring	Total food	663	1.044 ± 0.216	0	22.05	0.035	396	1.747 ± 0.345	0.309
	Fish prey	663	0.691 ± 0.194	0	20.07	0	396	1.157 ± 0.318	0
	Other prey	663	0.353 ± 0.106	0	22.05	0	396	0.590 ± 0.174	0.107
Fall	Total food	758	0.565 ± 0.152	0	20.08	0.005	402	1.066 ± 0.276	0.116
	Fish prey	758	0.437 ± 0.138	0	20.08	0	402	0.825 ± 0.255	0
	Other prey	758	0.128 ± 0.065	0	17.13	0	402	0.241 ± 0.121	0.039
Atlantic cod									
≤30 cm									
Spring	Total food	143	0.462 ± 0.087	0	3.66	0.340	126	0.525 ± 0.094	0.397
	Fish prey	143	0.000 ± 0.000	0	0.00	0	126	0.000 ± 0.000	0
	Other prey	143	0.462 ± 0.087	0	3.66	0.340	126	0.525 ± 0.094	0.397
Fall	Total food	161	0.554 ± 0.313	0	23.65	0.178	128	0.697 ± 0.390	0.270
	Fish prey	161	0.178 ± 0.288	0	23.65	0	128	0.224 ± 0.363	0
	Other prey	161	0.376 ± 0.133	0	9.57	0.112	128	0.473 ± 0.164	0.214
>30 cm									
Spring	Total food	632	0.765 ± 0.097	0	9.66	0.342	592	0.817 ± 0.102	0.385
	Fish prey	632	0.286 ± 0.083	0	9.66	0	592	0.305 ± 0.088	0
	Other prey	632	0.479 ± 0.058	0	7.77	0.185	592	0.511 ± 0.061	0.209
Fall	Total food	761	0.601 ± 0.102	0	14.12	0.149	684	0.669 ± 0.113	0.201
	Fish prey	761	0.331 ± 0.094	0	12.45	0	684	0.369 ± 0.104	0
	Other prey	761	0.270 ± 0.042	0	7.21	0.073	684	0.300 ± 0.046	0.105

fish, whereas no consistent pattern emerged between large and small Atlantic cod.

A significant proportion of the stomachs in the samples was empty, especially among silver hake (Tables 3, 4). Moreover, among those fish containing measurable amounts of food in their stomachs, the distribution of stomach content weight was strongly skewed towards small values. For these two reasons, the median stomach content weight was always considerably less than the mean weight (Table 5).

The mean and median stomach content weights within the entire population, which includes fish that had empty stomachs, were less than the corresponding values when only those fish containing measurable quantities of food were considered (last three columns of Tables 3 and 4; last two columns of Table 5). The differences were greater for silver hake than Atlantic cod, because of the large percentage of hake with empty stomachs. These data show that, even when the analysis is restricted to the fish that have recently fed (i.e., the fish with nonempty stomachs), the amount of food in the stomachs is, on the average, very much less than the maximum amount that the fish are physically capable of ingesting (as indicated by the maximum observed values, Table 5).

The mean stomach contents by season for each species, all sizes combined, are presented in grams and as a percentage of body weight in Tables 3 and 4. When the stomach contents are expressed in terms of weight (grams), the apparent importance of fish prey in the diet is greater than when the stomach contents are expressed as a percentage of body weight. This disparity occurs because the large, more piscivorous, fish contain a much greater weight of food in their stomachs, and have a disproportionate effect compared with the more numerous, but less piscivorous, small fish. This bias is eliminated if the stomach content weight is normalized to the weight of the fish (percent body weight) for the calculation of mean stomach contents. This also allows intercomparison of samples with different size-distributions of fish. We have, therefore, expressed the stomach content data as percent body weight for the analysis of diel changes in stomach fullness and daily ration.

Diel Changes in Stomach Contents

The diel feeding patterns of large and small silver hake appeared to differ. The weight of the stomach contents of small hake fluctuated over the 24-h day, but did not show any trends indicative of diel periodicity in feeding intensity during either spring or fall (Fig. 3). However, large hake exhibited a strong

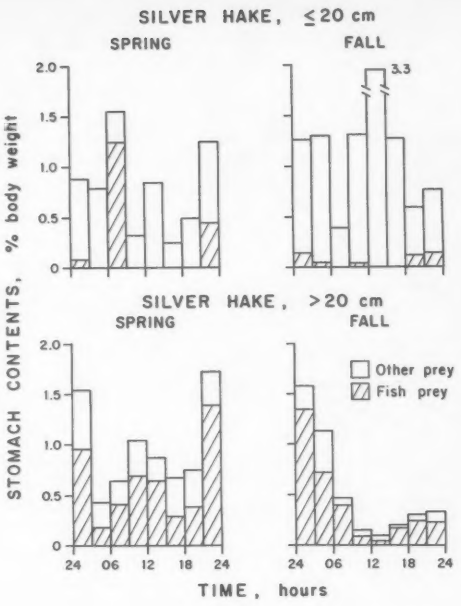


FIGURE 3.—Diel changes in "total stomach content weight," "fish prey," and "other prey" in the stomachs of small and large silver hake during spring and fall.

pattern of nocturnal feeding during the fall (Fig. 3). This pattern was less clear during spring, when comparatively large amounts of food were observed in the stomachs during the daytime. However, maximum amounts of food occurred at night, between 2100 and 0300.

Among small silver hake, the number of empty stomachs averaged 23.4% during spring over the 24-h day, with highest values observed between 1500 and 2400 (see Fig. 5). During the fall, the mean number of empty stomachs was 21.9%, with no apparent diel pattern. Among large hake, the number of empty stomachs averaged 40.4% during spring and 47.8% during fall. The percentage remained fairly constant throughout the day except for peaks between 1500 and 2100 during spring and 0900 and 1500 during fall. These peaks corresponded to the periods when the minimum mean weight of stomach content was observed (Fig. 3).

In contrast to silver hake, there were no apparent diel trends in the stomach contents of Atlantic cod (Fig. 4). The percentage of empty stomachs was lower in cod than in hake, and there was no diel pattern (Fig. 5). Among large cod, the percentage of empty stomachs over the day averaged 6.4% during spring

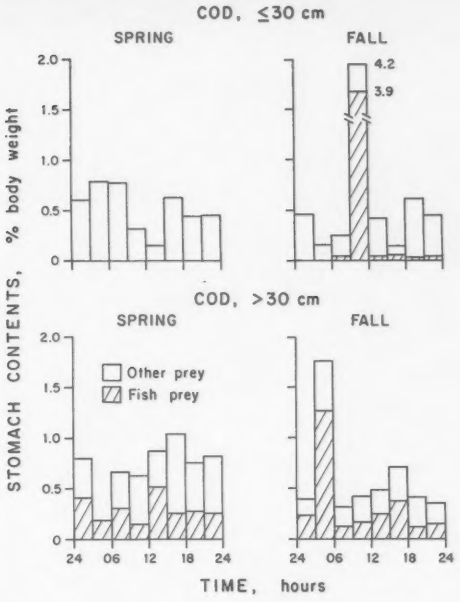


FIGURE 4.—Diel changes in "total stomach content weight," "fish prey," and "other prey" in the stomachs of small and large Atlantic cod during spring and fall.

and 10.2% during fall. Among small cod, the respective percentages were 10.6 and 14.7%.

Daily Ration

In order to describe the average feeding behavior of all fish in the samples, the mean stomach content weights, which included fish with empty stomachs, were used to estimate the mean feeding rate for each 3-h period during the day (Tables 6, 7). Ingestion estimates fluctuated considerably, and negative as well as positive values occurred. The negative ingestion estimates resulted when the decline in amount of food in the stomach from one period to the next was greater than predicted from the evacuation rate used in the calculation. Daily rations were obtained by summing the amount of food ingested during each 3-h period.

With the exception of small silver hake in the fall, the daily ration estimates for the two species were not greatly different: small hake, 1.82 and 4.65% BW during spring and fall, respectively; large hake, 2.40 and 1.92%; and large Atlantic cod 1.42 and 1.66% BW (Tables 6, 7). Overall, hake consumed more than large cod; the daily ration of small cod was not estimated because of the small sample size. The daily ration of small hake and large cod was higher, and of large hake was lower, during the fall than during

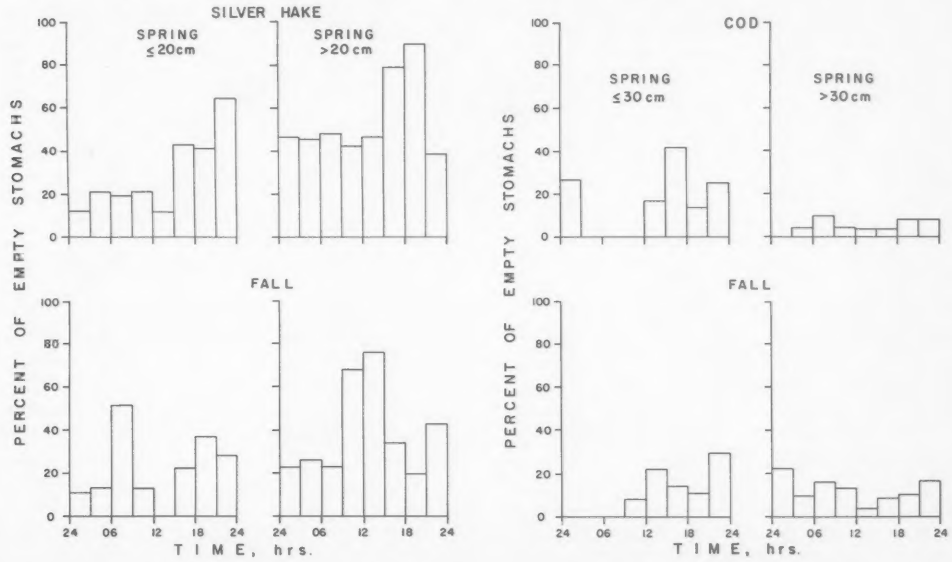


FIGURE 5.—Diel changes in the percentage of empty stomachs of silver hake and Atlantic cod collected during each 3 h time period.

TABLE 6.—Number of fish caught, amount (% BW) of food in the silver hake stomachs ($\bar{x} \pm$ standard error of mean), and estimated mean amount of food ingested during each 3-h period. BW = body weight.

	Time	Total no. of fish (No. of tows)	Total food		Fish prey		Other prey	
			Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)
Silver hake ≤20 cm								
Spring								
Temp = 7.63°C	24-3	136 (13)	0.888 ± 0.079	0.145	0.083 ± 0.024	−0.081	0.805 ± 0.078	0.207
R = 0.0947	3-6	101 (7)	0.795 ± 0.093	1.101	0.009 ± 0.007	1.430	0.786 ± 0.092	−0.329
	6-9	36 (4)	1.557 ± 0.400	−0.973	1.252 ± 0.412	−1.083	0.305 ± 0.078	0.110
	9-12	14 (4)	0.325 ± 0.135	0.693	0 ± 0.0	0	0.325 ± 0.135	0.693
	12-15	17 (2)	0.848 ± 0.124	−0.453	0 ± 0.0	0.008	0.848 ± 0.124	−0.461
	15-18	30 (5)	0.244 ± 0.089	0.360	0.007 ± 0.005	−0.001	0.237 ± 0.089	0.361
	18-21	128 (7)	0.497 ± 0.057	1.005	0.004 ± 0.004	0.505	0.493 ± 0.056	0.500
	21-24	34 (7)	1.249 ± 0.390	−0.060	0.443 ± 0.382	−0.288	0.806 ± 0.156	0.228
			$\bar{x}$ = 0.800	Σ = 1.818	$\bar{x}$ = 0.225	Σ = 0.510	$\bar{x}$ = 0.576	Σ = 1.309
Fall								
Temp = 11.94°C	24-3	145 (15)	1.262 ± 0.116	0.625	0.143 ± 0.062	−0.055	1.118 ± 0.095	0.682
R = 0.153	3-6	204 (16)	1.299 ± 0.106	−0.544	0.046 ± 0.033	−0.036	1.253 ± 0.102	−0.507
	6-9	35 (4)	0.385 ± 0.105	1.329	0 ± 0.0	0.037	0.385 ± 0.105	1.290
	9-12	31 (6)	1.309 ± 0.183	2.991	0.030 ± 0.030	−0.024	1.278 ± 0.187	3.016
	12-15	6 (3)	3.226 ± 0.692	−0.952	0 ± 0.0	0.012	3.226 ± 0.692	−0.963
	15-18	86 (8)	1.275 ± 0.168	−0.255	0.010 ± 0.007	0.138	1.266 ± 0.169	−0.394
	18-21	76 (11)	0.601 ± 0.102	0.487	0.117 ± 0.063	0.087	0.484 ± 0.086	0.399
	21-24	214 (17)	0.770 ± 0.079	0.967	0.144 ± 0.065	0.065	0.626 ± 0.053	0.901
			$\bar{x}$ = 1.266	Σ = 4.648	$\bar{x}$ = 0.061	Σ = 0.224	$\bar{x}$ = 1.205	Σ = 4.424
Silver hake >20 cm								
Spring								
Temp = 8.45°C	24-3	99 (16)	1.542 ± 0.408	−0.813	0.963 ± 0.319	−0.612	0.579 ± 0.274	−0.201
R = 0.104	3-6	46 (7)	0.430 ± 0.170	0.377	0.179 ± 0.153	0.321	0.251 ± 0.084	0.056
	6-9	60 (11)	0.639 ± 0.254	0.670	0.407 ± 0.246	0.460	0.232 ± 0.082	0.210
	9-12	92 (17)	1.043 ± 0.300	0.130	0.693 ± 0.275	0.153	0.350 ± 0.141	−0.024
	12-15	102 (15)	0.875 ± 0.227	0.038	0.639 ± 0.225	−0.210	0.236 ± 0.065	0.248
	15-18	79 (18)	0.673 ± 0.163	0.296	0.287 ± 0.128	0.201	0.386 ± 0.113	0.095
	18-21	78 (12)	0.747 ± 0.228	1.373	0.383 ± 0.171	1.292	0.364 ± 0.158	0.081
	21-24	107 (14)	1.726 ± 0.369	0.324	1.390 ± 0.369	−0.063	0.336 ± 0.083	0.388
			$\bar{x}$ = 0.959	Σ = 2.395	$\bar{x}$ = 0.618	Σ = 1.542	$\bar{x}$ = 0.342	Σ = 0.853
Fall								
Temp = 11.76°C	24-3	115 (19)	1.575 ± 0.359	0.161	1.340 ± 0.335	−0.162	0.235 ± 0.149	0.324
R = 0.150	3-6	85 (14)	1.134 ± 0.310	−0.317	0.724 ± 0.240	−0.086	0.411 ± 0.205	−0.231
	6-9	84 (13)	0.468 ± 0.234	−0.192	0.392 ± 0.235	−0.191	0.076 ± 0.023	−0.0006
	9-12	71 (9)	0.144 ± 0.070	0.009	0.096 ± 0.069	−0.023	0.048 ± 0.015	0.030
	12-15	70 (13)	0.099 ± 0.031	0.171	0.043 ± 0.025	0.178	0.055 ± 0.020	−0.007
	15-18	94 (18)	0.201 ± 0.122	0.218	0.171 ± 0.121	0.169	0.029 ± 0.014	0.052
	18-21	155 (23)	0.304 ± 0.090	0.178	0.245 ± 0.090	0.088	0.060 ± 0.013	0.089
	21-24	84 (18)	0.337 ± 0.132	1.689	0.227 ± 0.127	1.484	0.110 ± 0.031	0.205
			$\bar{x}$ = 0.533	Σ = 1.917	$\bar{x}$ = 0.405	Σ = 1.457	$\bar{x}$ = 0.128	Σ = 0.461

spring.

When the daily ration was estimated using an R value for fish prey derived from Equation (3) (Tables (6-8), then fish prey constituted 28.1 and 4.8% of the daily ration of small hake during spring and fall, respectively. In large cod, fish prey constituted 38.2 and 55.1% of the daily ration, whereas in large silver hake, fish prey constituted 64.4 and 76.0% (Tables 6-8). However, if the lower estimate of the evacuation rate for fish prey items is used in the calculation, the importance of fish prey in the diet of all groups was sharply reduced (Table 8). The effect on the total estimated daily ration was small for hake ≤20 cm, because this size class did not feed heavily upon fish prey. However, since large hake and large cod feed extensively upon fish prey, a change in the R value for this prey type significantly affected the total estimated daily ration (Table 8).

DISCUSSION

Application of the Elliott and Persson Model

The Elliott and Persson model was originally described for field samples collected in a restricted area from the same population over time. Present data were obtained from extensive surveys over large areas rather than intensive surveys of single populations. As applied here, the model provides a broad overview of ingestion by fish located over a very large geographic area. Resolution of this composite picture to include possible differences in fish behavior in different years or areas would have required additional intensive field surveys and was beyond the scope of the present study.

Daily ration estimates, which are based on field

TABLE 7.—Number of fish caught, amount (% BW) of food in the Atlantic cod stomachs ($\bar{x} \pm$ standard error of mean), and estimated mean amount of food ingested during each 3-h period. BW = body weight.

	Time	Total no. of fish (No. of tows)	Total food		Fish prey		Other prey	
			Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)
Atlantic cod ≤30 cm								
Spring								
Temp = 5.72°C	24-3	5 (2)	0.603 ± 0.241		0 ± 0.0		0.603 ± 0.241	
	3-6	14 (4)	0.790 ± 0.262		0 ± 0.0		0.790 ± 0.262	
	6-9	4 (1)	0.785 ± 0.235		0 ± 0.0		0.785 ± 0.235	
	9-12	24 (6)	0.316 ± 0.042		0.001 ± 0.001		0.314 ± 0.041	
	12-15	9 (3)	0.154 ± 0.103		0 ± 0.0		0.154 ± 0.103	
	15-18	7 (2)	0.635 ± 0.282		0 ± 0.0		0.635 ± 0.282	
	18-21	63 (10)	0.442 ± 0.053		0 ± 0.0		0.442 ± 0.053	
	21-24	17 (9)	0.451 ± 0.152		0 ± 0.0		0.451 ± 0.152	
			$\bar{x}$ = 0.522		$\bar{x}$ = 0		$\bar{x}$ = 0.522	
Fall								
Temp = 8.46°C	24-3	30 (11)	0.461 ± 0.113		0 ± 0.0		0.461 ± 0.113	
	3-6	6 (5)	0.151 ± 0.076		0.006 ± 0.006		0.145 ± 0.076	
	6-9	7 (5)	0.252 ± 0.083		0.040 ± 0.040		0.212 ± 0.090	
	9-12	6 (6)	4.213 ± 3.889		3.942 ± 3.942		0.271 ± 0.124	
	12-15	12 (7)	0.418 ± 0.150		0.039 ± 0.030		0.379 ± 0.126	
	15-18	24 (5)	0.140 ± 0.044		0.053 ± 0.026		0.087 ± 0.038	
	18-21	30 (7)	0.615 ± 0.111		0.028 ± 0.028		0.587 ± 0.108	
	21-24	46 (6)	0.448 ± 0.208		0.045 ± 0.021		0.403 ± 0.208	
			$\bar{x}$ = 0.837		$\bar{x}$ = 0.519		$\bar{x}$ = 0.318	
Atlantic cod >30 cm								
Spring								
Temp = 5.77°C	24-3	58 (16)	0.795 ± 0.125	−0.063	0.406 ± 0.126	−0.147	0.389 ± 0.061	0.084
R = 0.0769	3-6	64 (17)	0.575 ± 0.089	0.228	0.191 ± 0.075	0.166	0.384 ± 0.054	0.062
	6-9	81 (18)	0.660 ± 0.146	0.116	0.300 ± 0.122	−0.102	0.360 ± 0.066	0.219
	9-12	116 (20)	0.628 ± 0.086	0.410	0.147 ± 0.066	0.439	0.481 ± 0.059	−0.029
	12-15	88 (17)	0.865 ± 0.168	0.394	0.509 ± 0.170	−0.167	0.356 ± 0.052	0.561
	15-18	80 (16)	1.039 ± 0.183	−0.076	0.255 ± 0.135	0.076	0.784 ± 0.134	−0.152
	18-21	60 (20)	0.757 ± 0.121	0.245	0.270 ± 0.087	0.052	0.487 ± 0.100	0.192
	21-24	85 (22)	0.820 ± 0.151	0.161	0.261 ± 0.126	0.223	0.558 ± 0.096	−0.061
			$\bar{x}$ = 0.767	Σ = 1.415	$\bar{x}$ = 0.292	Σ = 0.540	$\bar{x}$ = 0.475	Σ = 0.876
Fall								
Temp = 9.30°C	24-3	91 (28)	0.398 ± 0.087	1.748	0.234 ± 0.084	1.304	0.164 ± 0.032	0.443
R = 0.114	3-6	94 (24)	1.763 ± 0.323	−1.108	1.271 ± 0.298	−0.926	0.492 ± 0.128	−0.182
	6-9	103 (25)	0.314 ± 0.060	0.230	0.119 ± 0.055	0.099	0.195 ± 0.029	0.130
	9-12	95 (24)	0.418 ± 0.092	0.220	0.168 ± 0.083	0.148	0.249 ± 0.047	0.072
	12-15	111 (31)	0.483 ± 0.085	0.438	0.245 ± 0.070	0.235	0.238 ± 0.050	0.203
	15-18	84 (22)	0.714 ± 0.158	−0.109	0.373 ± 0.158	−0.172	0.341 ± 0.048	0.063
	18-21	87 (20)	0.415 ± 0.061	0.071	0.119 ± 0.058	0.076	0.296 ± 0.034	−0.005
	21-24	96 (21)	0.355 ± 0.076	0.172	0.149 ± 0.066	0.151	0.206 ± 0.046	0.021
			$\bar{x}$ = 0.608	Σ = 1.662	$\bar{x}$ = 0.335	Σ = 0.915	$\bar{x}$ = 0.273	Σ = 0.745

TABLE 8.—Upper and lower estimates of R for fish prey, and the effect upon the estimated daily ration, where: $R_{\text{fish, max}} = 0.0406\, e^{0.111t}$; $R_{\text{fish, min}} = 0.00406\, e^{0.111t}$, and $R_{\text{other}} = 0.0406\, e^{0.111t}$. Basic data from Tables 6 and 7. BW = body weight.

	Fish prey (% BW)	Other prey (% BW)	Total (% BW)	Fish prey % of total
Silver hake ≤20 cm				
Spring				
$R_{\text{fish, max}}$	0.510	1.309	1.818	28.1
$R_{\text{fish, min}}$	0.051	1.309	1.360	3.8
Fall				
$R_{\text{fish, max}}$	0.224	4.424	4.648	4.8
$R_{\text{fish, min}}$	0.022	4.424	4.446	0.5
Silver hake >20 cm				
Spring				
$R_{\text{fish, max}}$	1.542	0.853	2.395	64.4
$R_{\text{fish, min}}$	0.154	0.853	1.007	15.3
Fall				
$R_{\text{fish, max}}$	1.457	0.461	1.917	76.0
$R_{\text{fish, min}}$	0.146	0.461	0.607	24.1
Atlantic cod >30 cm				
Spring				
$R_{\text{fish, max}}$	0.540	0.876	1.415	38.2
$R_{\text{fish, min}}$	0.054	0.876	0.930	5.8
Fall				
$R_{\text{fish, max}}$	0.915	0.745	1.662	55.1
$R_{\text{fish, min}}$	0.092	0.745	0.837	11.0

stomach content data, require information on digestion rate of the various prey types. Equation (3) is based on maximum evacuation rates observed in the laboratory for small, easily digested food items. Evacuation rates determined from this equation should provide an upper limit to estimates of ingestion rates (Table 8). Since there are indications that fish prey may be digested more slowly, the daily ration was also estimated using the lowest observed values of evacuation rate for fish prey (Table 8). This reduced the estimate of ingestion of fish prey by a factor of 10, and provided a lower limit for the probable ingestion rates. The potential significance of this 10-fold range in the R value is well illustrated by the case of silver hake >20 cm, where during the spring, for example, fish prey constituted 66.2% of the stomach contents by weight, yet the calculated ingestion of fish ranged from as much as 64% to as little as 15% of the diet, depending on the R value used.

This illustrates the need for additional information on the digestion rates of a variety of different prey items, particularly fish prey. If different prey types are digested at different rates, then the static picture of the food web as provided by stomach content analysis may not truly indicate the relative rates of flow of the different elements through the food web.

Food Habits and Stomach Content Weight

The food habits and stomach content weight of silver hake and Atlantic cod in the present study are in general agreement with the results of other studies (Rae 1967, 1968 a, b; Tyler 1971; Vinogradov 1972; Daan 1973; Langton and Bowman 1980).

Rae (1967, 1968a, b) provided a detailed description of the food habits of Atlantic cod in the North Sea, the Faroes, and Iceland, and Vinogradov (1972) described the food habits of silver hake in the North Atlantic. These studies are not directly comparable with the present study because they presented the diet by the frequency of occurrence of prey, not by weight. However, Rae reported that in general, fish prey were seldom eaten by cod <21 cm, but became increasingly important in the diet as the cod grew larger. Cod >50 cm fed mostly on fish. Vinogradov also found that hake became increasingly piscivorous with increasing size, and that hake >40 cm fed almost entirely on fish. These results are consistent with the present study.

Langton and Bowman (1980) have described the food habits of silver hake and Atlantic cod (>20 cm in length) that were caught during 1969-72 in the same area as the present study. Silver hake averaged 27.5 cm in length, their mean stomach content weight was 2.5 g, and the proportion of fish in the diet was 70.9% by weight. Atlantic cod averaged 54.7 cm in length, their mean stomach content weight was 27.9 g, and fish prey constituted 64.0% of the diet by weight. These are very close to our present results with hake >20 cm [mean length = 31.2 cm, mean weight of stomach contents = 2.9 g (0.79% BW), proportion of fish in the diet = 81.7% by weight], and cod >30 cm [mean length = 60.9 cm, mean weight of stomach contents = 29.6 g (0.68% BW), and mean proportion of fish in the diet = 62.3% by weight]. These results imply that no large-scale changes in the mean weight of stomach contents in the two species occurred in the study area between 1969 and 1976. Possible changes in factors such as prey species or prey size, however, are not evaluated in this report.

The weight of the stomach contents of 15-40 cm Atlantic cod from Passamaquoddy Bay, New Brunswick, was reported by Tyler (1970: figure 7). During spring, the stomach content weights were very similar to those of 15-40 cm cod reported here. However, during late summer-fall, cod in Tyler's study generally had more food in their stomachs (usually >1% BW; range 0.4-2.7% BW) than fish in this study.

Daan (1973) investigated the food habits of Atlantic cod from the northern and southern portions of the North Sea. In general, the weights of the stomach contents of cod (divided into 10 cm size classes) in his study were considerably higher than in the present study (compare Daan's table XI with our Table 4). Daan's samples were collected principally during the daytime, but he considered that diel feeding periodicity was not significant in his study area. In addition, Daan's cod were more piscivorous than the cod collected during the present study (compare his figure 2 with our Table 4). He found that fish prey became increasingly important in the diet with increasing size of cod. These results are in agreement with the present study.

The percentage of empty stomachs observed during our study is in agreement with those reported by Tyler (1971), Daan (1973), and Langton and Bowman (1980).

Diel Changes in Stomach Contents

Edwards and Bowman (1979) and Bowman and Bowman (1980) concluded that silver hake >20 cm were principally nocturnal feeders. Results of the present study also indicate that hake >20 cm feed more intensively at night. However, the lack of significant diel changes in the stomach content weight of hake ≤20 cm indicates that these small fish may feed continuously throughout the day.

The lack of evident feeding periodicity in Atlantic cod was consistent with an extensive study by Rae (1967) and with observations by Daan (1973). Sattersdal (1967) reviewed several studies on feeding periodicity in gadoids, and also concluded that with cod, feeding may take place at any time during the night or day.

Daily Ration

Daan (1973) estimated the daily ration of Atlantic cod from the North Sea, where the mean temperature (5°-9°C) was similar to that experienced by Atlantic cod in the present study. Although these fish, on the average, contained more food in their stomachs, the estimates of the daily food intake were relatively

lower than in the present study, declining from 1.3% BW/d in a 40 cm cod to 0.8% BW/d in a 60 cm fish, to 0.5% BW/d in a 100 cm fish.

Grosslein et al. (1980) used energy budget calculations to estimate the daily ration of six major fishes (Atlantic cod, silver hake, yellowtail flounder, haddock, herring, and mackerel) in the northwest Atlantic during 1963-72. The mean daily ration of silver hake was calculated to be 1.3% BW/d; the daily ration of Atlantic cod was 0.9% BW/d. During 1963-72, the daily food consumption by hake averaged 24.2% of the total consumption by the six species; the daily ration of the cod was 3.7% of the total.

A study by Edwards and Bowman (1979) estimated the daily ration of silver hake to be 3.1% BW/d, and Atlantic cod to be 2.3% BW/d. These authors also concluded that the hake is a major consumer in the food web of the northwest Atlantic.

These daily ration estimates compare with mean upper and lower estimates of 3.2 and 2.9% BW/d for silver hake $\leq$20 cm, 2.2 and 0.8% BW/d for hake $>$20 cm, and 1.5 and 0.9% BW/d for Atlantic cod $>$30 cm in the present study (Table 8, assigning spring and fall estimates equal weight for the determination of mean ingestion).

Differences in the estimates of daily ration in the above studies reflect differences in the mean stomach content weight of the fish, as well as differences in the methods used to estimate daily ration. However, estimates of daily ration in silver hake were consistently found to be greater than in the Atlantic cod.

The high proportion of empty stomachs among silver hake, and the fact that the average amount of food in the stomachs of both silver hake and Atlantic cod were small, is intriguing from an ecological viewpoint. For example, the results may simply reflect the innate feeding behavior of these two predators, i.e., they feed at a modest rate even when food is plentiful and easily obtained. On the other hand, the results could mean that food is either scarce, or if abundant, difficult for the fish to locate or capture. It would be of interest, in future work, to explore the question of whether the major fish predators in the northwestern Atlantic are food limited, since this will greatly affect the importance of different predator-prey links in the food web and the intensity of competition among different fishes for food.

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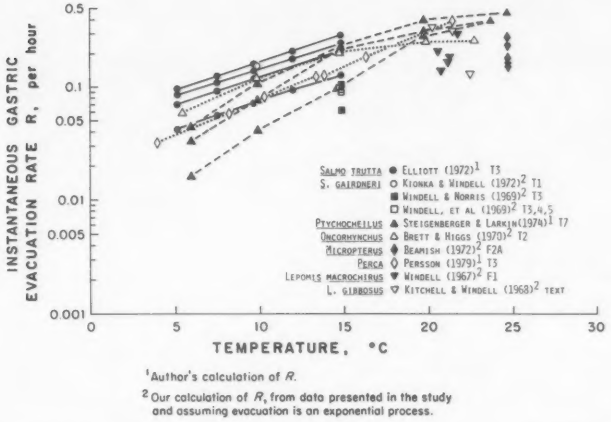
APPENDIX 1

Estimation of the Instantaneous Gastric Evacuation Rate, *R*

A number of factors may affect the instantaneous rate of gastric evacuation, *R*. These include temperature, food type, food particle size, meal size, fish size, autolysis of food in the stomach, swimming activity, prestarvation, experimental stress, experimental error, and time lags between ingestion and the beginning of gastric evacuation.

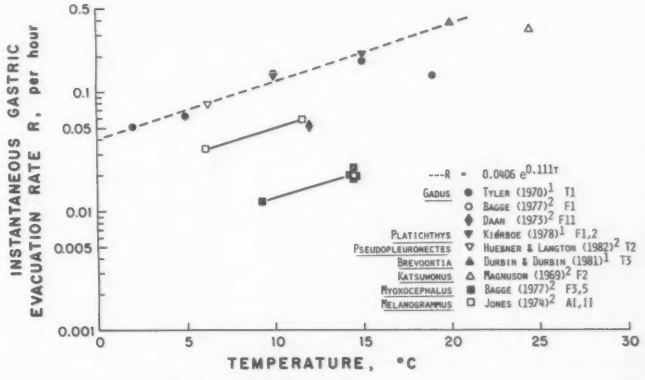
R values from the more complete studies of marine and freshwater fishes are presented as a function of temperature in Appendix Figures 1 and 2.



[1] Author's calculation of *R*.

[2] Our calculation of *R*, from data presented in the study and assuming evacuation is an exponential process.

APPENDIX FIGURE 1.—The relationship between the instantaneous gastric evacuation rate (R, per hour) and temperature in several marine fishes. Note that the body temperature of *Katsuwonus* was probably greater than that of the water temperature shown here. Dashed line and equation based on data from Tyler (1970, 2°-15°C), Kiørboe (1978), Durbin and Durbin (1981), and Huebner and Langton (1982). Source of data, where T = Table, F = Figure, and A = Appendix is shown.



[1] Author's calculation of *R*.

[2] Our calculation of *R*, from data presented in the study and assuming eve evacuation is an exponential process.

APPENDIX FIGURE 2.—The relationship between the instantaneous gastric evacuation rate (R, per hour) and temperature in several freshwater fishes. Sources of data as in Appendix Figure 1.

TEMPERATURE

The gastric evacuation rate R appears to follow an exponential or power curve relationship with temperature t (Elliott 1972):

$$R = ae^{bt}. \quad (1)$$

Evacuation rates of brown trout that were fed small, rapidly digested prey (*Gammarus*, *Baetis*, Oligochaetes, chironomids), were described by the relationship

$$R = 0.053\ e^{0.112\,t}. \quad (2)$$

In further experiments with other foods (*Protonemura*, *Hydropsyche*, *Tenebrio*) Elliott (1972) found that the intercept (a) in Equation (2) was dependent on prey type, but that the slope (b) was constant and independent of prey type. Data from other freshwater and marine fishes (within their preferred temperature range) indicate that the value of b is fairly close to that found by Elliott for the brown trout (Appendix Table 1; $\bar{b} = 0.115$). At temperatures outside the preferred range, evacuation rates were depressed (i.e., Atlantic cod at 19°C, Tyler 1970). The value of a varies widely in different studies, apparently because of the different prey types used.

The fastest evacuation rates have been reported for a variety of small food organisms. These rates, when adjusted for differences in experimental temperature, were fairly similar among several marine and freshwater fishes: Atlantic cod, fed 0.5 g chunks of shrimp (*Pandalus*) tails (Tyler 1970); the flounder *Platichthys*, fed 0.1 g polychaetes (Kiørboe 1978); winter flounder *Pseudopleuronectes*, fed 0.5-1.0 cm pieces of squid (Huebner and Langton 1982); Atlantic menhaden, fed 80 μm diatoms (Durbin and Durbin 1981)[1]; brown trout, fed 1 and 15.7 mg *Gammarus*, 0.9 and 7.8 mg *Baetis*, 0.33 and 3.3 mg chironomids, and 29 mg oligochaetes (Elliott 1972); sockeye salmon, fed small commercial pellets (Brett and Higgs 1970); pumpkinseed sunfish fed damselfly larvae (Kitchell and Windell 1968); and bluegill sunfish fed 180 mg crayfish (Windell 1967) (App. Figs. 1, 2).

The marine species ingesting these readily digested foods followed a common R-temperature relationship (App. Fig. 1):

$$R = 0.0406\ e^{0.111t}. \quad (3)$$

The a and b values are similar to those observed by Elliott (1972) for the brown trout feeding on easily digested foods (0.053 and 0.112, respectively); b is also similar to the overall mean value in Appendix Table 1.

APPENDIX TABLE 1.—Slope (b) of the relationship between the instantaneous evacuation rate (R, per hour) and temperature (°C) for several freshwater and marine fishes, where: $R = ae^{bt}$. The intercept (a) varies with food type.

Species	Slope (b)	Experimental temp. range (°C)	Author
Brown trout, *Salmo trutta*	0.112	5.2-15.0	Elliott (1972)[1]
Northern squawfish, *Ptychocheilus oregonesis*	0.131	6.0-24.0	Steigenberger and Larkin (1974)[1]
Perch, *Perca fluviatilis*	0.140	4.0-21.7	Persson (1979)[1]
Cod, *Gadus morhua*	0.106	2.0-15.0	Tyler (1970)[1]
Ophiocephalus punctatus	0.137	2.0-28.0	Gerald (1973)[2]
Haddock, *Melanogrammus aeglefinus*	0.095	6.1-11.6	Jones (1974)[2]
Flounder, *Platichthys flesus*	0.081	10.0-15.0	Kiørboe (1978)[1]
	$\bar{x} \pm \sigma = 0.115 \pm 0.022$		

[1]Based on author's calculations of R.
[2]Based on our calculation of R from data in study, and assuming that evacuation is an exponential process.

FOOD TYPE

Studies have shown that there are differences in evacuation rates with different food types. While these results may reflect inherent differences in the digestibility of the food, they may also indicate an interaction between food type, particle size, and meal size. In practice, these factors may be difficult to resolve, particularly when the results of different studies are being compared.

However, certain small prey organisms were digested significantly more slowly than those cited above. This may reflect the chemical composition of the prey. For example, slower digestion of *Tenebrio* and *Hydropsyche* by bluegill and brown trout was attributed to the high fat content of these organisms (Kitchell and Windell 1968; Elliott 1972). Pure fat retards

[1]Gastric evacuation rate R in menhaden was estimated from the feces elimination rate R'.

evacuation in rainbow trout (Windell et al. 1969) as well as in vertebrates other than fishes (Quigley and Meschan 1941). Artificial pelleted food, which is high in organic content, is also digested more slowly than natural food (Windell and Norris 1969; Windell et al. 1969). The degree of external protection of the prey can also affect the digestion rate. For example, rainbow trout digested the caddisfly *Arctopsyche*, and the cottid *Enophrys* digested *Calliphora* larvae, more slowly than other prey types, evidently because the integument of the prey was resistant to the penetration of the gastric juices (Reimers 1957; Western 1971). MacDonald et al. (1982) also reported that the shell in *Yoldia* retarded the evacuation rate in several marine fishes.

The lowest evacuation rates which have been observed were from fish feeding on fish flesh, usually in fairly large particle and meal sizes [Atlantic cod, fed whole 14 g sprats, meal sizes about 3.7% BW (Daan 1973), Atlantic cod, fed to satiation on 2-3 g pieces of greater weever (Bagge 1977); haddock *Melanogrammus aeglefinus*, fed saithe, 1-7% BW (Jones 1974); skipjack tuna, fed 10.2 g osmerids, 8.6% BW (Magnuson 1969); *Ophiocephalus*, fed small fish 7.9% BW (Gerald 1973); sea scorpion fed to satiation on 5 g pieces of greater weever (Bagge 1977); northern squawfish, fed small *Salmo* (Steigenberger and Larkin 1974); largemouth bass, fed 1.22 g emerald shiners, 2-8% BW (Beamish 1972) (App. Figs. 1, 2)]. These reductions in R may be significant: for example, with Atlantic cod and sea scorpion, the instantaneous evacuation rates for fish flesh were only about one-tenth those predicted by Equation (3) for easily digested foods.

Whether these reduced evacuation rates were due primarily to the food type (fish), or to the large particle sizes, compared with those of the small prey which were digested more rapidly, cannot be determined from the data.

Additionally, in a few studies, after several food types were tested individually and found to have similar evacuation rates, meals composed of mixtures of these food types were given (Windell 1967; Elliott 1972). The evacuation rate of the mixed meal was not significantly different from that of the individual food types. However, evacuation rate of mixed meals containing food types which have individually different R values does not appear to have been investigated.

FOOD PARTICLE SIZE

The exponential model predicts that the evacuation rate, R, depends only on the weight of food in the stomach, i.e., $dW/dt = -RW$. Thus R should be independent of food particle size. A meal of a given weight, composed of a number of small particles, should be evacuated at the same rate as a meal of equal weight, but composed of a single large particle. However, if digestion occurs at the surface of particles, then the surface area as well as the weight or volume of the food may influence digestion. A surface-area dependent model predicts that small particles should be digested more rapidly than large particles because of their greater surface area per unit volume, i.e., $dW/dt = -RW^{2/3}$.

Few studies have considered the effect of particle size on R.

Elliott (1972) found no effect of food particle size on the gastric evacuation rates of brown trout fed small invertebrates. However, the particle sizes tested were quite small and may have been below some critical size which has a measurable effect on R.

The evacuation rates of Atlantic cod that were fed whole fish or large pieces of fish flesh (Daan 1973; Bagge 1977) were lower than those of Atlantic cod fed small pieces of shrimp (Tyler 1970). However, it is not clear whether this difference is an effect of food particle size or food type.

Swenson and Smith (1973) examined gastric evacuation of walleye and sauger fed 0.8, 1.1-1.9, and 3.1-5.0 g minnows. The two smallest size classes were evacuated at a significantly faster rate than the 3.1-5.0 g fish. However, the difference between the evacuation rates was small, and the different food particle sizes therefore did not have a major effect on the evacuation rate.

MEAL SIZE

Experimental data on the effect of meal size on the gastric evacuation rate is conflicting.

The exponential model predicts that gastric evacuation is not affected by meal size. Studies using small prey as the food have confirmed this prediction: Brown trout, fed 0.06-0.5% BW meals of *Gammarus* and 0.35-1.4% BW of *Tenebrio* (Elliott 1972); pumpkinseed sunfish, fed 1.2 and 2.7% BW of damselfly naiads (Kitchell and Windell 1968); Atlantic cod fed 0.25-0.78% BW on shrimp tails (Tyler 1970); flounder, fed variable meal sizes of polychaetes (Kiørboe 1978); and Atlantic menhaden, fed 0.7-7.0% BW on the diatom *Ditylum* (Durbin and Durbin 1981). Some studies using fish flesh as the food also indicated that meal size did not affect R: Sea scorpion, fed 5.5-11.1% BW on greater weever (Bagge 1977); skipjack tuna, fed various meal sizes averaging 8.6% BW on fish (Magnuson 1969).

However, some authors have suggested that in their studies (where fish flesh was the food), evacuation was slower for large meals than for small (Steigenberger and Larkin 1974; Jones 1974). These authors found that significant time lags, on the order of hours, elapsed between ingestion and the onset of gastric evacuation. Similar lags have been reported by other investigators who used fish as the prey type (Daan 1973; Gerald 1973). Some question therefore remains as to whether meal size had a direct effect on R in these studies, or whether the primary effect of increasing meal size was to cause a progressive increase in the time lag before the onset of gastric evacuation.

EFFECT OF MULTIPLE MEALS

Most digestion rate studies have examined stomach evacuation rates following a single meal. However, in nature most fish do not normally feed in this manner, but rather feed on a more or less continuous, or a periodic, basis. In this situation the time for food to pass through the stomach and the relation between the amount of food in the stomach and evacuation rates will be more complex.

Elliott (1972) fed brown trout three meals, 6 h apart. He then determined the stomach contents 4 h after the last meal. This amount was in good agreement with that calculated from the exponential model, and Elliott concluded that multiple meals, and the presence of food already in the stomach, did not affect R or the exponential model of gastric evacuation.

Tyler (1970) fed Atlantic cod three meals, 24 h apart at 5°C. He too used an exponential model to predict the amount of food remaining in the stomach after the third meal. The actual amount was slightly, but significantly, lower (by about 7%) than the predicted. He concluded that, overall, the fit was adequate.

In the studies of Kiørboe (1978) and Huebner and Langton (1982), individual fish were fed a number of meals in sequence. Although the data showed a significant degree of variability, reflecting differences in the voluntary food intake of the fish, the mean values followed a common exponential relationship, which implies that multiple meals did not affect R.

CONCLUSIONS

In summarizing this brief discussion, several conclusions can be drawn:

1) The exponential model of gastric evacuation provides a good fit to most experimental data, and also provides good estimates of ingestion rate when used in the Elliott and Persson (1978) model.

2) The two factors which are known to most strongly influence the instantaneous gastric evacuation rate R are temperature and food type. Multiple meals do not affect the value of R. The available evidence indicates that particle size and meal size probably do not affect R (at least with small prey items), but these questions need further investigation.

3) The slopes (b) of the R-temperature relationships among several marine and freshwater fishes were similar, although the intercepts (a) varied according to the type of food.

FACTORS AFFECTING THE DISTRIBUTION, ABUNDANCE, AND SURVIVAL OF *PANDALUS JORDANI* (DECAPODA, PANDALIDAE) LARVAE OFF THE OREGON COAST

PETER C. ROTHLISBERG[1] AND CHARLES B. MILLER[2]

ABSTRACT

Abundance, distribution, and survival of larval pink shrimp, *Pandalus jordani*, differed between 1971 and 1972. Consistent southwest winds in the February-March spawning season of 1972 kept surface flow onshore and larvae closer to the coast than did the mixed winds of 1971. The early season of 1972 was warmer than that of 1971, and development was faster: Zoea V were prevalent at the end of April 1972, compared with median advancement to Zoea III by early May in 1971. Corresponding to the lesser dispersal and faster development of 1972, survival was substantially better than in 1971.

Overall larval survival at settlement time appears from analysis of long-term fishery data and upwelling indices to have some dependence upon the strength of June to August upwelling. Extrapolation from laboratory studies suggests that is because survival is enhanced by the temperatures consistently 12°C and below maintained by strong upwelling. Timing of spawning and development interacts with timing of the flow regime. Summer upwelling generally keeps the habitat suitably cold for optimal development and survival and returns larvae to seaward for settlement roughly at the beds from which they were spawned.

Hjort (1914, 1926) was the first to suggest the importance of larval mortality in establishing year class strength of marine fish. This concept has been useful generally, and, in particular, larval mortality most fully explains fluctuations of stocks in species both short-lived and fecund. However, larval mortality per se is only one component of total mortality. Factors affecting parental stock size, fecundity, spawning and hatching rates, larval dispersal, metamorphosis, and postlarval and prerecruitment mortality will also generate year-to-year variation in population size. In many marine animals these life history phases are in totally different habitats and have very different durations.

Given the complexity of the life cycle and the variety of habitat features which can therefore act importantly, it is not surprising that sound explanations of year class variations have begun to emerge only now. Long time series of catch data and well-developed understanding of oceanographic processes are both required. Interesting recent examples include Southward et al. (1975), Boudreault et al. (1977), Driver (1978), and Dow (1978). Creation of indices of coastal upwelling strength (Bakun 1973) has given us an important variable for study of factors influencing year class strength in marine populations. Upwelling acts in several ecologically significant ways, affecting temperature, salinity, nutrient concentrations, and current patterns. Enhancement of productivity in nearshore regions is well documented (Steemann Nielsen and Jensen 1957; Ryther and Menzel 1965; Ryther 1969). However, not only enhancement of productivity, but the specific changes in flow caused by upwelling can have important effects. Success of life stages is likely to be related to the time of onset of seasonal upwelling, intensity and duration of upwelling, and even to details of its intermittency. Effects can be negative. Lasker (1978) found that upwelling dispersed the food of larval northern anchovy, *Engraulis mordax*, reducing food availability below levels established in the laboratory (Lasker 1975) as minimal. Coe (1956), Winnor (1966), Lough (1976), and Nelson et al. (1976) have all shown that upwelling can both improve and reduce survival by transport of larvae toward or away from favorable habitat.

We report here an attempt to evaluate the importance of larval survival to the year class strength of the pink shrimp, *Pandalus jordani*, and to determine which aspects of ocean dynamics affect larval survival. First, larval distribution and abundance of *P. jordani* were ascertained by field sampling. Second, apparent survival in several spawning seasons was compared with laboratory studies of the effects of habitat factors (Rothlisberg 1979) and with the hydrographic regime during sampling to estimate the degree to which environmental factors determined

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larval survival in the field. Finally, an attempt was made to examine the contribution of year-to-year variation in ocean conditions during the postspawning season to variation in year class strength. Ocean conditions were primarily characterized by Bakun's upwelling indices.

MATERIALS AND METHODS

Sampling for *Pandalus jordani* larvae was carried out during 32 cruises from January 1971 to August 1972 along a transect extending 60 nmi from the coast off Newport, Oreg., U.S.A. (Newport Hydroline; stations designated NH-1, etc. according to distance from coast; Fig. 1). Sampling was at approximately fortnightly intervals (Fig. 2). On all but one cruise the 24.4 m RV *Cayuse* was used. In March and April 1972 a more extensive grid sampling was conducted on two cruises along a series of seven transects from Tillamook Head (I, Fig. 1) south almost to the Siuslaw River (VII). These transects extended 30 mi from the coast.

Temperature and a salinity sample were taken at the surface at each station, and temperatures at lower depths were obtained by bathythermograph (BT) cast to the bottom or a maximum of 150 m. Bottom salinity was obtained from a bottle sample collected at the greatest extent of the BT cast. On 9 of the 11 cruises in 1972 (C7205D and C7207E excluded), drift bottles were released. Plankton was collected by stepped oblique tows to near the bottom or to a maximum of 150 m with a 0.7 m diameter bongo net (cylinder-cone nets 5.1 m long of 0.571 mm Nitex[3] with effective filtering area to mouth area ratio of 8:1). The tows with three to five steps lasted 10 to 25 min, depending on depth. At towing speeds of 2 to 3 kn the nets filtered 600 to 1,000 m^3; specific amounts were determined from TSK flowmeters in the mouth of each net. Depths were maintained by a 40 kg kite-otter depressor (Colton 1959) and recorded by time-depth recorder. Samples were preserved at sea with formaldehyde. Only the port side sample was analyzed from each pair, a total of 367 from the two years. Because of their relatively low density, the entire sample was sorted for shrimp larvae.

The National Weather Service gathers hourly wind data at a recording anemometer located at the base of the south jetty at Newport, Oreg. We used this data in their stored form (north-south and east-west vector components; m/s) to generate progressive vector diagrams.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

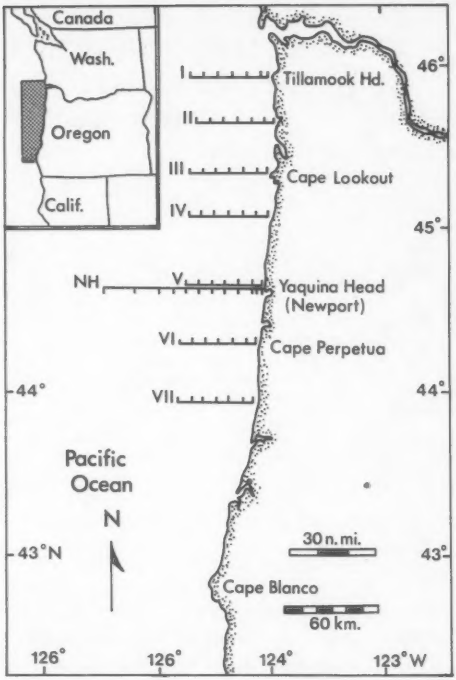


FIGURE 1.—Sampling transects off the Oregon coast. Newport Hydro (NH) line with stations: 1, 3, 5, 10, 15, 20, 25, 30, 35, 40, 50, and 60 nmi from the coast. Transects I-VII with stations 1, 5, 10, 15, 20, 25, and 30 nmi from coast. Transect V and NH line overlap.

RESULTS

Seasonal Wind, Current, and Temperature Regimes, 1971 and 1972

Progressive vector diagrams for wind from January through July in 1971 and 1972 (Fig. 3) show that the two years differed in several respects. In February 1971 winds were mixed, while in 1972 the southwest winds typical of winter were consistent. Southwest winds dominated in March 1971, except for a spell of northwest wind from the 15th to the 21st. March winds in 1972 were mostly from the southwest, but less intense. There were a few 1-d reversals to northwest wind. April in both years was transitional, and a short spell of northwest wind initiated the upwelling season. Winds of the upwelling season, May through August, were stronger in 1972 than in 1971.

Comparison of upwelling indices for 1971 and 1972 with the 25-yr average for 1946-71 puts them in long-

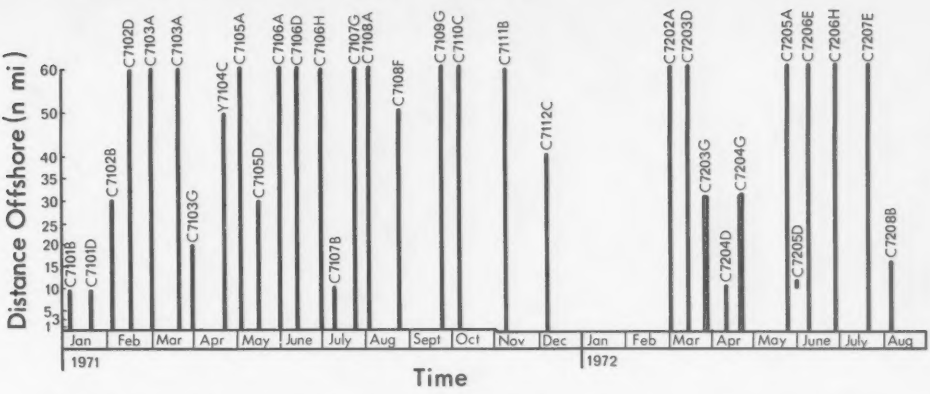


FIGURE 2.—Date and offshore extent of 32 cruises sampling larval *Pandalus jordani* from January 1971 to August 1972.

term perspective. These monthly indices (Bakun 1973, footnote 4) estimate the magnitude of the offshore component of Ekman transport mtons/s per 100 m coast) from mean monthly sea surface, geostrophic winds based on pressure fields. Deviations from the long-term mean (Table 1) imply that surface flow onshore in the first quarter of 1971 was below average, while that of 1972 was near normal. Upwelling in 1971 was less than normal, while that of 1972 was close to the long-term mean.

The northward Davidson Current was well demonstrated by the drift of bottles released in March and early April. There was also an onshore component which produced high return rates in those months (mean for March and early April = 47%; Fig. 4). By late April currents acquired a large southward component, and an offshore component reduced return rates (19.8% for late April through August; Fig. 4). Surprisingly, a considerable northward component remained in all months in the zone very close to the coast, as implied by returns from the 1 to 5 nmi stations in all periods except late May and early August.

In February through April 1971, temperatures varied between 8° and 10°C inside 20 nmi (Fig. 5). From late April through July they increased to between 14° and 15°C due to increased sunshine and lack of strong upwelling. The sharp, temporary decrease of early June corresponded to a pulse of upwelling in late May 1971 (Fig. 3). Nearshore temperatures in 1972 were more constant and warmer in the early part of the larval season than in 1971, ranging between 10° and 12°C. We attribute that to the strong onshore flow of late winter in that year. Temperatures rose slightly in spring but were held below the highs reached in late June of 1971 by the stronger upwelling conditions of 1972.

TABLE 1.—Upwelling indices by year and quarter for 1971 and 1972 along with the anomalies from a 25-yr average (from Bakun 1973, see text footnote 4).

	1973		1972	
	Index	Anomaly	Index	Anomaly
Entire year	1	10	− 2	7
First quarter (Jan.-Mar.)	−33	20	−49	3
Second quarter (Apr.-June)	26	−5	29	−2
Third quarter (July-Sept.)	33	−15	42	−5

Larval Distribution and Abundance of *Pandalus jordani* in 1971

Zoeae I, II, and III were found first on 16 February. They were widely distributed but most abundant at 5, 10, and 15 nmi (Fig. 6). In early March all larvae were within 20 nmi with highest density at 5 nmi; most were recently hatched, but there were some Zoeae II's, III's, and IV's. The cruise of 20 March appeared to coincide with the peak of larval hatching, Zoea I predominating and most abundant within 20 nmi of shore. The late March cruise was abbreviated because of bad weather. However, all larvae found at the 3 and 5 nmi stations were Zoea I. By 22 April the *P. jordani* were dispersed as far as 50 nmi offshore, but the peak of abundance was still at 5 nmi and consisted mostly of Zoeae II's and III's. A few

[4]A. Bakun, Pacific Environmental Group, Southwest Fisheries Center, NMFS, NOAA, c/o Fleet Numerical Oceanography Center, Monterey, Calif., pers. commun. February 1982.

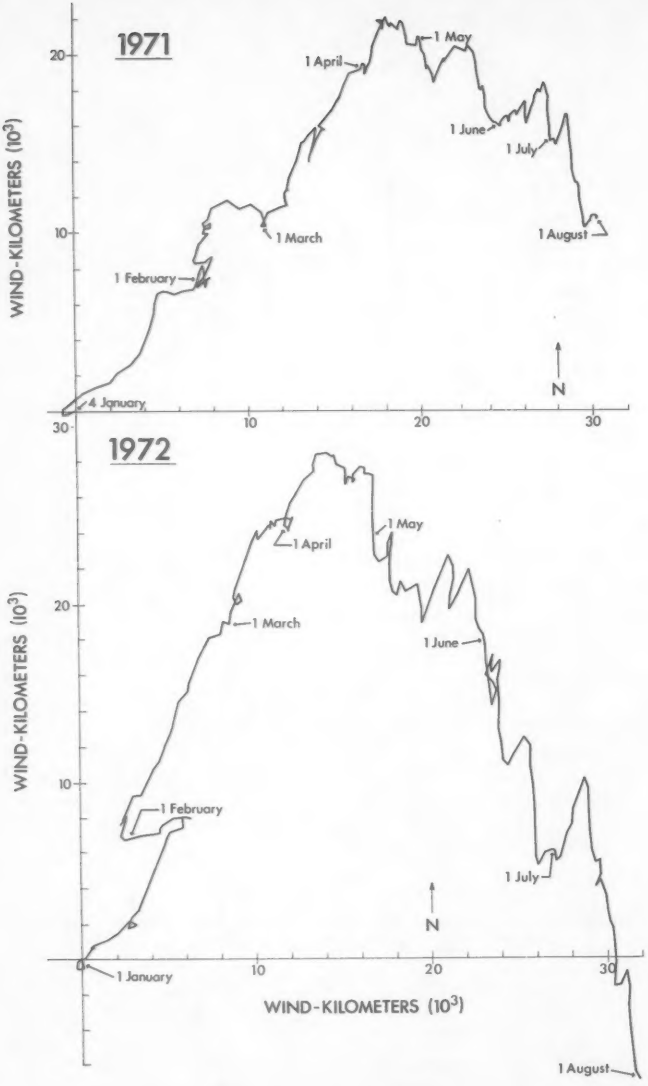


FIGURE 3.—Progressive vector diagrams for wind at Newport, Oreg., 1 January-1 August 1971 and 1972.

Zoeae VI's and VII's were caught at the 15 nmi station. On the early May cruise there were two centers at 5 and 50 nmi with young stages predominant at both. Samples collected 14 May contained a few intermediate and later larvae between 5 and 30 nmi. On 1 June, larvae were widely distributed between 10 and 60 nmi and were Zoeae VI to XIII. Larval abundance, though greater than in mid-May, was still low. Even greater dispersion was seen on 12 June (3 to 60 nmi), but there was a peak at 25 nmi. The cruise of 28 June produced the only two juveniles of the season at 5 and 15 nmi. Other larvae in late zoeal stages (X to XIII) were found between 10 and 40 nmi. No larvae or juveniles were found on 6 or 21 July.

To simplify the depiction of distribution of specific larval stages, abundances (no./1,000 m^3) were

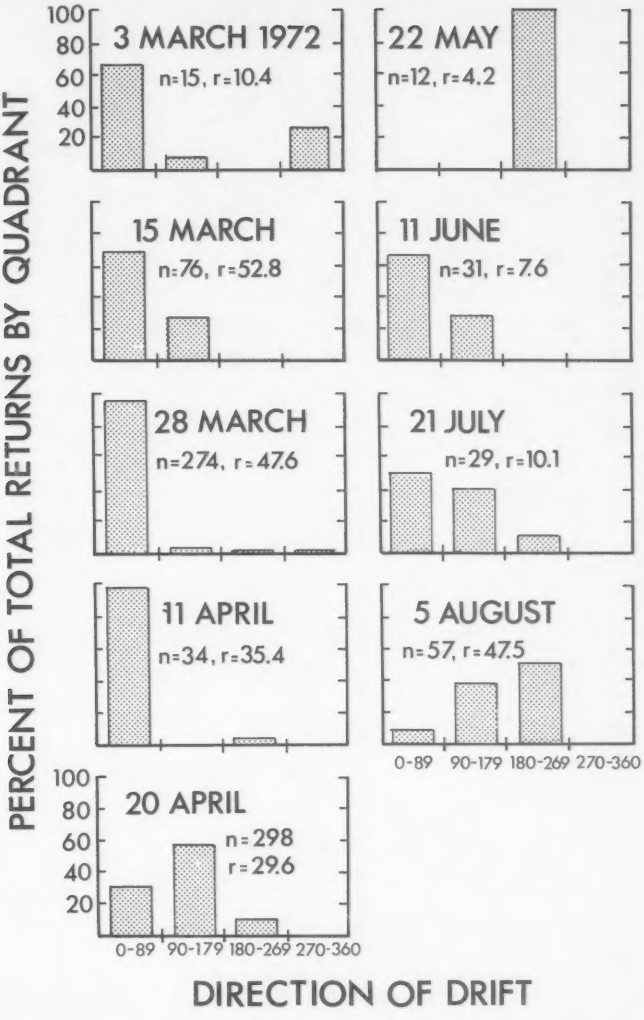


FIGURE 4.—Drift bottle-returns, 1972. Number, rate of return, and direction of drift summarized by quarterly components (from data supplied by M. J. Hosie, Fish Commission of Oregon, and W. Gilbert, Oregon State University School of Oceanography).

summed for each station over all cruises (Fig. 7). In 1971, Zoea I, though most abundant inshore, was spread over the entire 60 nmi of the transect. This trend continued to Zoea V, but increasing numbers appeared in the two seaward stations for II through V. By Zoea VI numbers were much diminished and most larvae were outside 15 nmi. This trend persisted through Zoea XIII. Small captures of late larvae and juveniles make generalizations for them difficult.

Larval Distribution and Abundance of *Pandalus jordani* in 1972

No cruises were made in 1972 until 4 March, when small numbers of young larvae (I and II) were found between 3 and 15 nmi (Fig. 6). On 16 March there were many Zoea I at 3 and 5 nmi and lower numbers farther out. Small numbers of Zoeae II and III were also present. A 30-mi transect in late March showed the center of abundance was at 10 nmi; mostly they

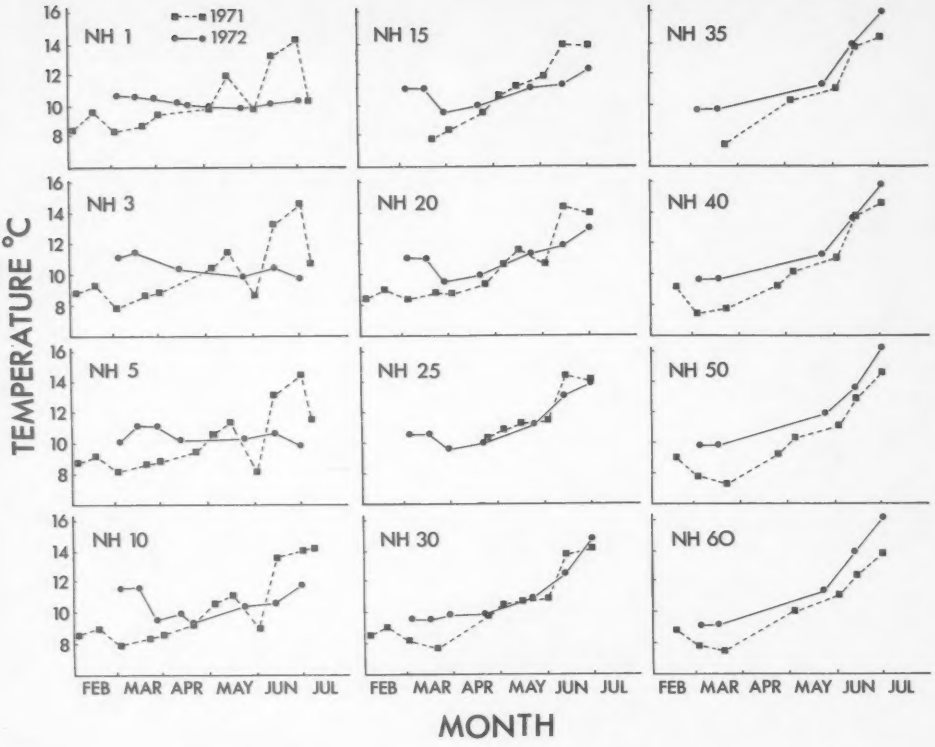


FIGURE 5.—Surface seawater temperatures at 12 sampling stations (NH-1 to NH-60) for February-July 1971 and 1972.

were Zoea III. The peak of larval hatching had apparently passed by that date. Larvae were present at the 1 nmi station for the first time and were present at all stations to 20 nmi. This contrasts to 1971, when *P. jordani* larvae were never found so close to shore. The 11 April cruise was curtailed for rough seas at 10 nmi. The most abundant stages were III's and IV's, but all stages from I to VIII were present. On 20 April stages I to XI were scattered between 5 and 30 nmi with VI to VIII most common. The distribution on 22 May was displaced offshore and spread between 10 and 45 nmi. Development was well advanced, and the first juveniles of the season were found at 25 and 30 nmi. Zoeae X to XII were dominant. Larvae on 11 June were advanced, older than XI, and distributed from 5 to 60 nmi with a peak between 10 and 20 nmi. Many juveniles were caught in a night tow at 15 nmi.

Figure 7 shows that early stages were generally less dispersed seaward in 1972 than in 1971. Zoeae I to IV were found only inside 15 nmi. Older larvae were found farther offshore, but rarely extended beyond 40 nmi. Late larvae (XIII) and early juveniles, though present in small numbers, were more abundant than in 1971 and were most abundant between 15 and 30 nmi.

Coastal Distribution and Abundance

All seven 30-nmi transects from Tillamook Head to the Siuslaw River were completed in late March 1972, but, due to bad weather, only the northern six were sampled in late April. As on the Newport line (Transect V), early larvae were most numerous inside 15 nmi, extending in to the 1 nmi stations in March (Fig. 8) over the whole grid. Larvae were most numerous at the 1 and 5 nmi stations, significantly more so than elsewhere as indicated by analysis of concordance of rank order of the stations according to larval density ($W = 0.62$; df = 7,7; $P<0.01$; see

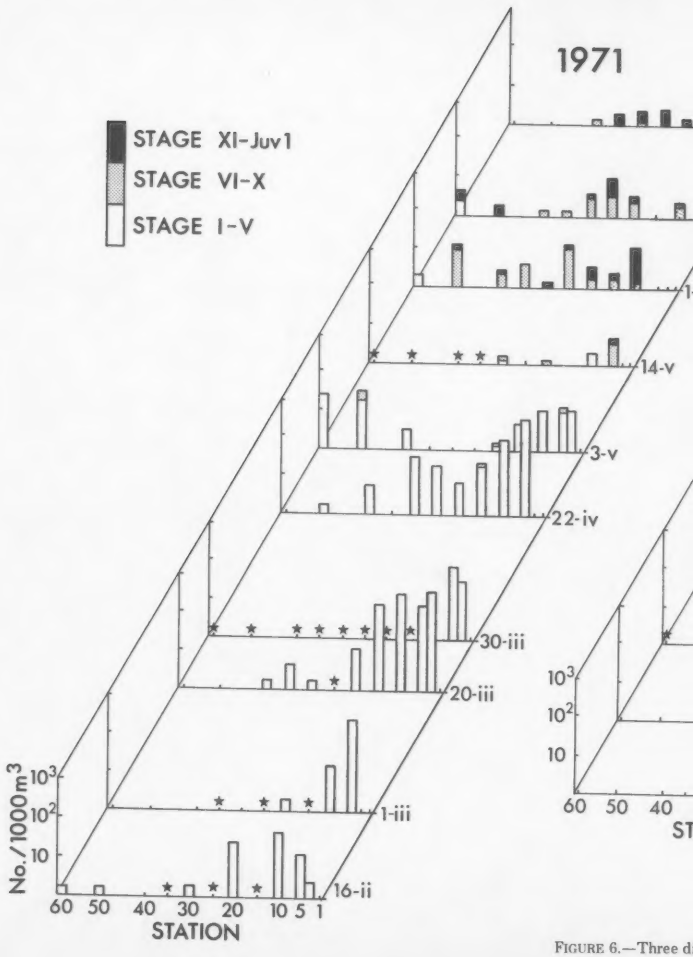
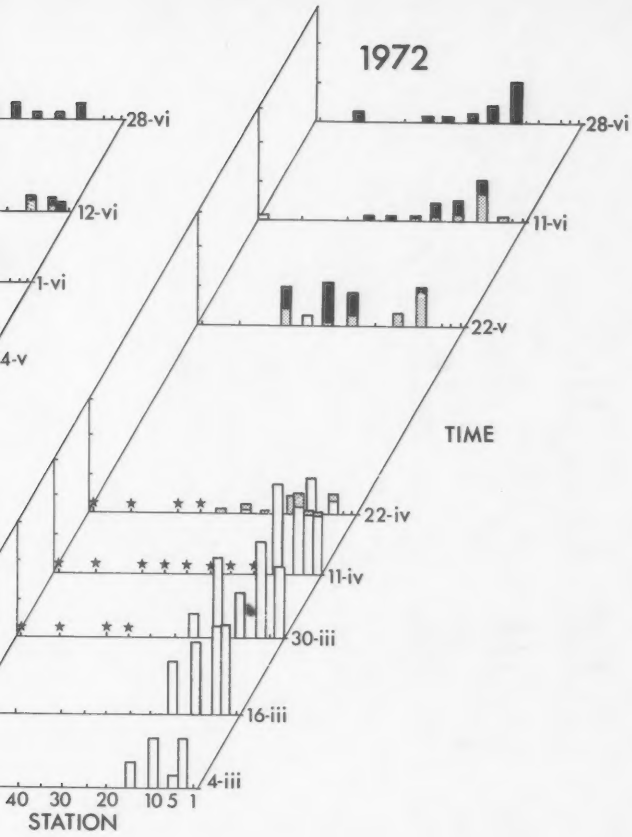


FIGURE 6.—Three d



Three dimensional display of larval distribution and abundance with time in 1971 and 1972.

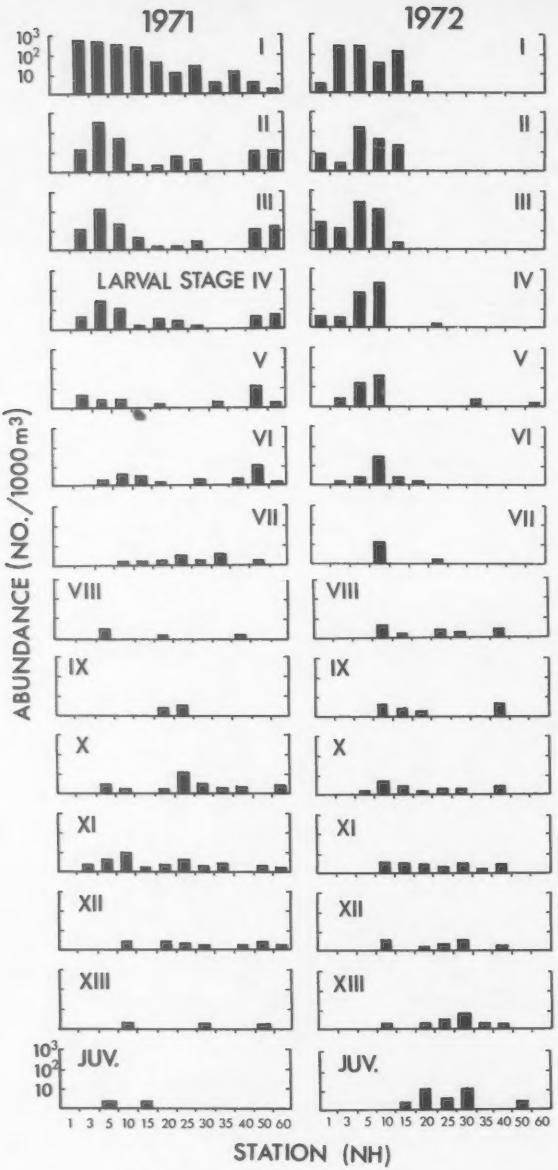


FIGURE 7.—Stage-specific larval distribution and abundance over all cruises in 1971 and 1972.

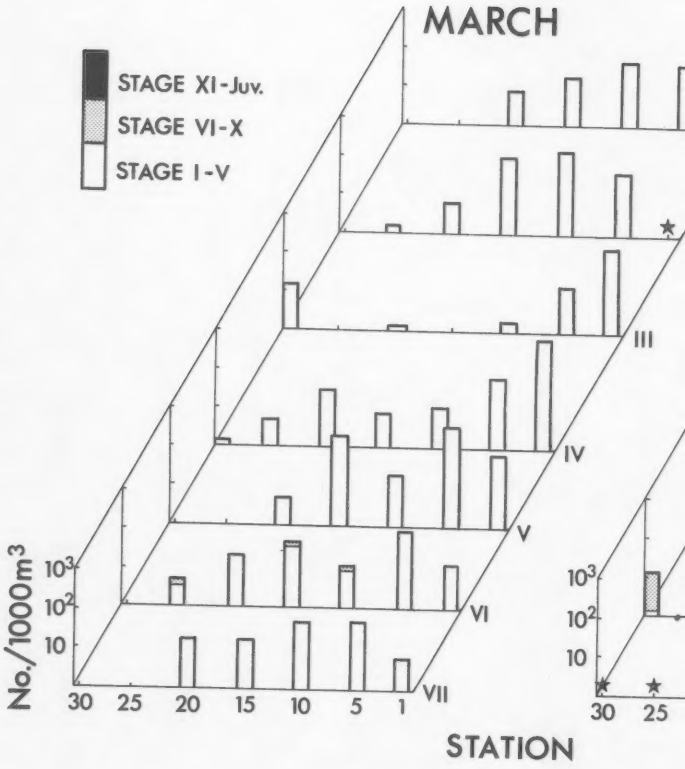


FIGURE 8.—Alongshore and offshore larval distributio

ribution and abundance in March and April 1972.

Tate and Clelland 1957). Overall larval abundance also varied between transects, IV and V having higher total numbers of larvae than the rest (1,093 and 718/1,000 m³ compared with ca. 250). Offshore displacement and dispersion of larvae had occurred by late April. Larvae were most numerous at the 10 nmi station, and many were collected out to 30 nmi. Concordance among transects with respect to rank order of stations was less than in March but still significant ($W = 0.43$; df = 7,6; $P < 0.01$). Larval numbers were reduced from March. Transects VI and I had the most larvae (418 and 232/1,000 m³ compared with <100 in the others).

The gradient of larval age along the coast was evaluated by summing abundance of each stage within transects (Fig. 9). March showed no consistent gradient, but there were considerable differences in median stage among transects. Medians for transects V and VI were 3.28 and 3.43, respectively. Others averaged 2.0. By April transects were more uniform in this respect. Median stage was 4.9 with a low of 4.2 and high of 5.8. The median increased 2.4 stages from March to April. While transects were more uniform, there was a wider range of stages in April with a slight increase in occurrence of older larvae in more southerly transects (IV to VI).

Onshore-offshore distribution was characterized by summing stage abundance at equivalent stations between transects for each cruise (Fig. 10). Zoeae I to IV predominated in March and were most abundant within 15 to 20 nmi. By April older larvae were dispersed outside 5 nmi.

Field Estimates of Larval Growth Rates

The two years differed in the rate of change of developmental stage frequency. Development can be followed roughly by successive estimates of the median stage in the pooled samples for each cruise (arrows in Fig. 11). In early cruises of 1971 larvae already were widely dispersed and subject to temperatures below 9°C in the whole region (Fig. 5). Cold persisted until late April, and median stage only in-

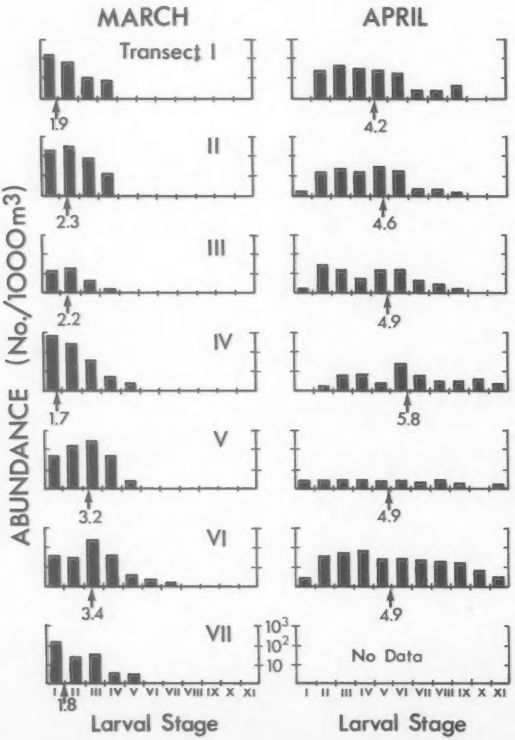


FIGURE 9.—Stage-specific larval distributions and abundance in March and April 1972. Larval abundance summed by stage within transects.

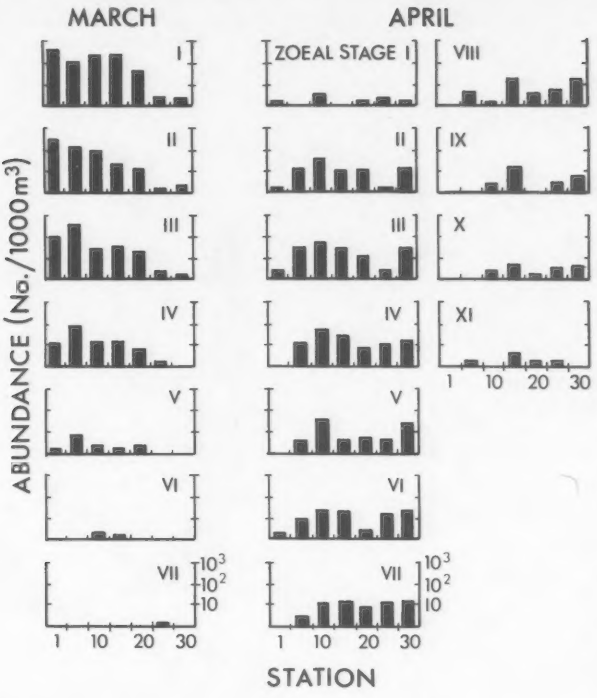


FIGURE 10.—Stage-specific larval distribution in March and April 1972. Larval abundance summed by stage over all transects.

creased to III by 4 May. There was rapid increase in median stage between 22 April and 1 June 1971, coinciding with rapid increase in surface temperature through May. In early cruises of 1972, larvae were confined to stations inshore of 20 nmi. Temperatures at those stations were about 2°C warmer than in 1971, and development was greater through 22 April, when median stage was V. Individuals up to Zoea XI were already present, which did not occur in 1971 until after the May spurt in development. Faster development in 1972 corresponded to water temperatures consistently higher than in 1971 from mid-March until June. By May of both years larvae were mostly dispersed between 10 and 50 nmi. Over that range temperatures were about the same and increasing from early May through June. Despite this, the increase in median stage slowed through June in both years. The median stage on 29 June was nearly XII in 1971 and XIII in 1972. The difference is not significant, and Zoea X through juvenile stages were present on that date in both years.

Larval Survival—Estimates from Field Sampling, 1971 and 1972

To assess larval survival in the field, total abundance was calculated for each larval stage over all cruises and stations (no./1,000 $m^3 \times$ sampled depth = no./1,000 m^2). In each year the total number of Zoea I was taken to be 100% of the larval hatch, and the number of each successive stage was expressed as a percent of that hatch (Fig. 12). Sampling effort was very similar between the two years in respect to timing and total number of cubic meters of water filtered (72,246 m^3 in 1971; 67,979 m^3 in 1972), so that the difference in survival probably was not an artifact.

We caught 1,653 Zoea I in 1971 and 530 in 1972. There is a reversal in this estimate from the order of the years in respect to hatch as estimated from egg counts in the commercial catch. Table 2 shows that the latter estimate was quite close in the two years: 1.75×10^{12} and 2.20×10^{12} in 1971 and 1972, respec-

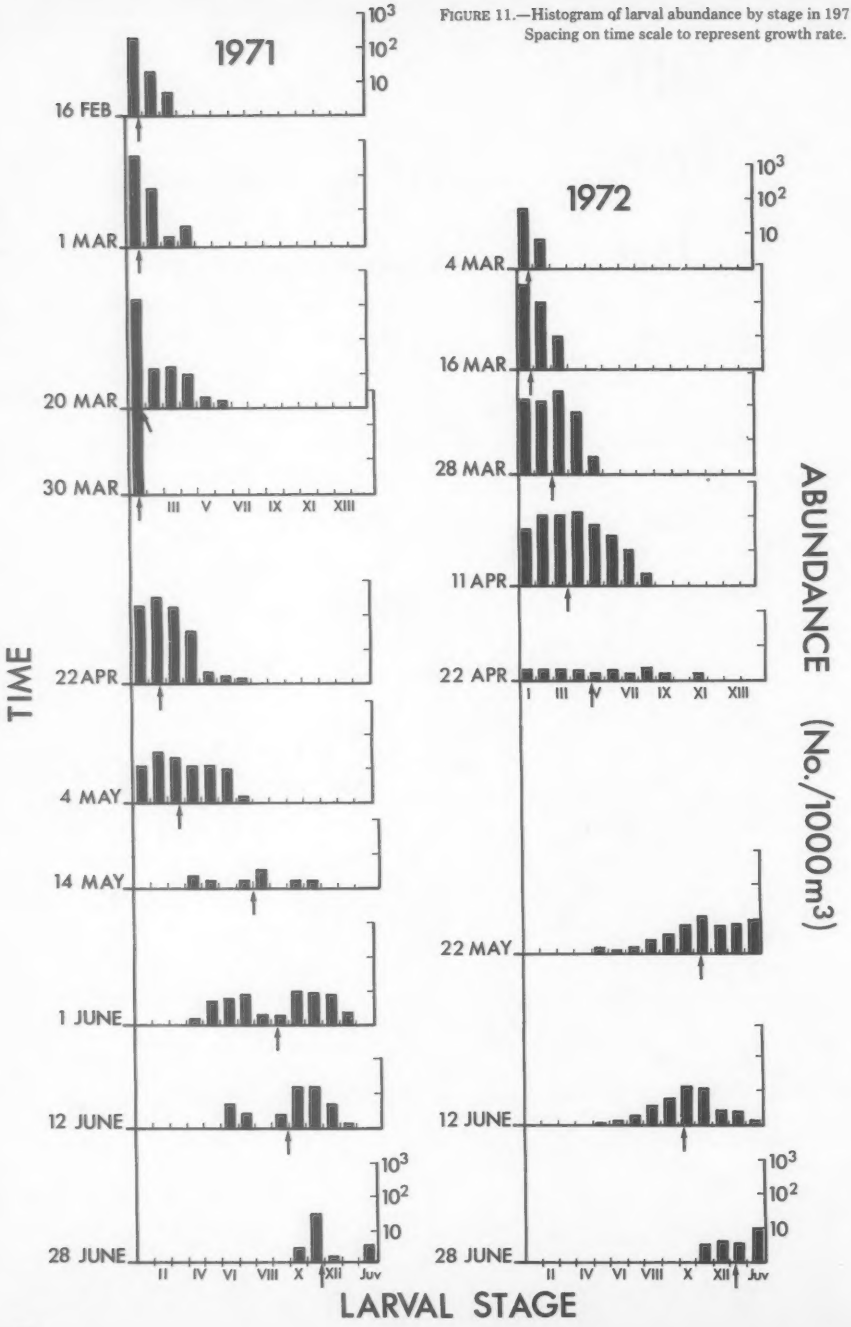


FIGURE 11.—Histogram of larval abundance by stage in 1971 and 1972. Spacing on time scale to represent growth rate.

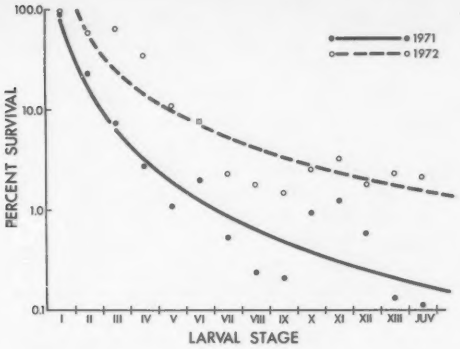


FIGURE 12.—Larval survival (percent) based on total numbers at each stage caught in the plankton sampling along NH line.

tively. Compared with the long-term variation in the commercial estimate of egg number, 1971 and 1972 were both close to average (mean 1961-80 = 1.93). In 1971, only 26.9% survived to Zoea II and <1% survived past Zoea VII. Only two Stage I juveniles (Rothlisberg 1980) were found in 1971, representing 0.17% of the hatch. In 1972 over 64% survived through Zoea III, with numbers and percentages decreasing gradually with age. Five Stage I juveniles were caught, 1.06% of the hatch. Percent surviving to the juvenile phase in 1972 was an order of magnitude higher than in 1971. This is not, of course, simply a comparison of two versus five survivors. There was a consistent difference between the years throughout the developmental sequence. Some survival estimates from the decreasing abundance at successive stages are shown at the bottom of Table 2. Such estimates depend on the assumption that reproduction is relatively synchronous (Mullin and Brooks 1970; Fager 1973). In both years the main pulse of hatching of *P. jordani* occurred within a relatively limited period, essentially synchronously.

Some of the variability of percent survival at individual stages (Fig. 12) can be due to the relationship between sampling frequency and molting frequency (mean intercruise period was 14.5 d, while mean intermolt period is 6.8 d, a ratio of 2.1:1). Stages can effectively be passed by the bulk of the population between two samplings. A simulation model of survival through stages of development and time was developed to illustrate this effect. The model imposed an intermolt period of 6 d over the entire

TABLE 2.—Estimates of larval survival (e^{-it}) from fishery data supplied by Fish Commission of Oregon (J. Robinson, see text footnote 5) and from field estimates of larval abundance $i = \ln (N_t/N_0)/t$ where $t = 1.5$ yr, the interval from hatching to recruitment to the commercial gear, i_{juv} = calculation for first year instantaneous mortality after recruitment to the bottom, from stomach analysis of hake, *Merluccius productus*, by Gotshall (1969, 1972); i_{larval} = instantaneous larval mortality as a proportion of the total instantaneous mortality (i) with instantaneous juvenile mortality (i_{juv}) held constant, see text. $t = 1.274$ yr (100 d), estimated time of larval period in plankton; $t = 0.364$, period between calculations of N_0 and N_t in 1971; $t = 0.263$, period between calculation of N_0 and N_t in 1972.

Year	$N_0 \times 10^{12}$	$N_t \times 10^9$	$N_t/N_0 \times 10^4$	$-\ln N_t/N_0$	i	i_{juv}	i_{larval}	$e^{-it} \times 10^4$
1961	2.45	0.50	2.04	8.50	5.66	1.50	24.30	12.8
1962	1.25	1.10	8.80	7.04	4.69	1.50	18.96	55.4
1963	2.30	0.33	1.43	8.85	5.90	1.50	25.58	9.0
1964	4.20	2.60	6.19	7.39	4.93	1.50	20.26	38.8
1965	0.75	0.75	10.00	6.91	4.61	1.50	18.51	62.7
1966	2.95	1.20	4.07	7.81	5.20	1.50	21.78	25.6
1967	0.80	1.25	15.62	6.46	4.31	1.50	16.87	98.3
1968	2.25	1.30	5.78	7.46	4.97	1.50	20.50	36.3
1969	1.00	0.75	7.50	7.20	4.80	1.50	19.55	47.2
1970	2.15	3.00	13.95	6.58	4.38	1.50	17.28	87.8
1971	1.75	0.25	1.43	8.85	5.90	1.50	25.60	9.0
1972	2.20	1.95	8.86	7.03	4.69	1.50	18.94	55.7
1973	1.85	1.66	8.97	7.02	4.68	1.50	18.89	56.5
1974	3.14	2.70	8.60	7.06	4.71	1.50	19.05	54.1
1975	3.24	1.98	6.11	7.40	4.93	1.50	20.30	38.4
1976	1.51	0.88	5.83	7.45	4.96	1.50	20.47	36.7
1977	1.50	0.64	4.27	7.76	5.17	1.50	21.61	26.8
1978	2.28	0.22	0.96	9.25	6.16	1.50	27.03	6.1
1979	0.72	0.30	4.17	7.78	5.19	1.50	21.69	26.2
1980	0.47	0.50	10.64	6.85	4.56	1.50	18.27	66.9
Mean								42.52
Estimation of larval survival, from larval abundance (no./1000 m³)								
1971	140,040	236	16.85	6.38	—	—	17.51	8.25
1972	40,146	475	118.32	4.44	—	—	16.88	98.02

length of the development and an instantaneous daily mortality rate (i) of 0.0788, the mean observed, overall rate of the two sampling years. This mortality was constant over all stages and constant within the molt cycle. The mortality rate was incorporated in a simple exponential decay formula to estimate survival rate over time ($N_t = N_0 e^{-it}$). Two hatching-time distributions were used: 1) A standard Normal distribution with 10^6 individuals released over 20 d, and 2) a severely peaked distribution with 850,000 of the 10^6 released over 5 d around median hatch time. We feel the latter distribution most accurately reflects hatching of *P. jordani* in the field.

The population was sampled in the model at various intervals, and the sequence of abundance of successive stages was determined by summing the abundance of each over all samples, just as we have done with the field estimates. These model stage abundances were presented in Figure 13. As would be expected, sampling more than once within an intermolt period (every 4 d) tends to overestimate survival to each larval stage. Sampling every 9 d (1.5 times the intermolt period) consistently underestimated larval numbers and survival. The severely peaked distribution of larval hatching times resulted in an oscillating estimate of larval survival. Magnitude of the oscillation was related to the degree of phase agreement between the sampling and molting. In all cases, however, whether the number of larvae was over- or underestimated at any particular stage, the survival rate based on sums of estimates of abundance paralleled the "actual" rate.

Table 3 summarizes the time between cruises, the estimated surface temperatures for each intercruise period (taken from Fig. 5), and an estimated intermolt period based on larval rearing experiments (Rothlisberg 1979). The shortest period between two cruises over the 2-yr sampling period was 8 d (22-30 May 1972), while the average was 14.5 d. Surface temperature for the larval period was rarely below 8°C (expected intermolt period = 8,08 d) and was 10° between 22 and 30 May 1972 (expectation = 7.0 d). The mean ratio of interval between cruises to intermolt period was 2.1, indicating that the survival estimates of this study would be low to an extent. Larvae could progress more than two stages between some cruises.

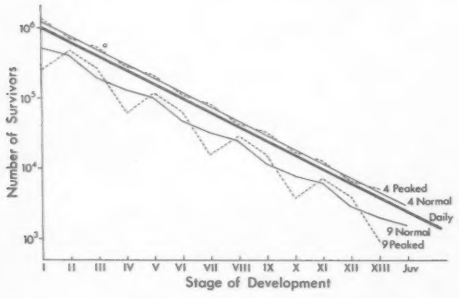


FIGURE 13.—The effect of sampling interval and larval hatching distribution on estimates of larval abundance and survival rate. Heavy line indicates "actual" survival rate; 4-normal, sampling standard normal distribution of larval hatch every 4 d; 9-normal, sampling every 9 d; 4-peaked, sampling peaked distribution of larval hatch every 4 d; 9-peaked, sampling peaked distribution every 9 d (see text for further explanation).

TABLE 3.—Period between cruises (days), estimated temperature for the period (from Fig.5), intermolt period at the temperature (from Rothlisberg 1979), and the ratio between cruise (IC) period and intermolt (IM) period.

Sampling date	Intercruise period (days)	Temperature (°C)	Intermolt period (days)	Ratio IC/IM
1971				
16 Feb.				
1 Mar.	13	9	7.3	1.8
20 Mar.	19	9	7.3	2.6
30 Mar.	10	8	8.1	1.2
22 Apr.	23	9	7.3	3.2
4 May	12	10	7.0	1.7
14 May	10	11	6.6	1.5
1 June	16	11	6.6	2.4
12 June	11	12	6.4	1.7
28 June	16	14	6.3	2.5
Mean				2.1
1972				
4 Mar.				
16 Mar.	12	11	6.6	1.8
28 Mar.	12	11	6.6	1.8
11 Apr.	14	10	7.0	2.0
22 Apr.	11	10	7.0	1.6
22 May	30	10	7.0	4.3
30 May	8	10	7.0	1.1
12 June	13	10	7.0	1.9
28 June	16	10	7.0	2.3
Mean				2.1
Overall Mean				2.1

Estimates of Larval Survival from Commercial Landings

Long-range trends in larval survival of *P. jordani* were sought from Oregon fishery statistics to put the apparent differences in larval survival between 1971 and 1972 into perspective. Data on number of ova and of age 1 shrimp were provided by J. Robinson[5]. He estimated ova from adjusted estimates of numbers of females in samples of the April commercial landings and an empirical length to fecundity relationship (Robinson 1971). Numbers of age 1

[5]J. Robinson, Oregon Department of Fisheries and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. February 1982.

shrimp were estimated from commercial landings 1.5 yr later (November) when they were fully recruited to the fishing gear. Figure 14 shows the fluctuations in these data from 1961 to 1980. Instantaneous rate of total mortality, i, was calculated from the data according to formulae of Ricker (1958). Results are shown in Table 2.

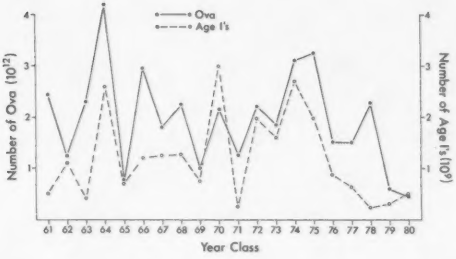


FIGURE 14.—Number of ova and number of age I shrimp recruited to the commercial fishery 1.5 yr later, by year class (Robinson unpubl. data).

Separation of the planktonic larval mortality from total mortality required an estimate of juvenile mortality. Gotshall (1969,1972), using an analysis of stomach contents of Pacific hake, *Merluccius productus*, which has been shown to prey on *P. jordani* without respect to age, has calculated that juvenile mortality rate, i_{juv}, is 1.50/yr. Proportioning total instantaneous mortality within the 18 mo from hatching to first harvest was done according to:

$$i = \frac{0.274\ (i_{larval}) + 1.226\ (i_{juv})}{1.5},$$

where $i = \ln(N_t/N_0)/t$, with $t = 1.5$ yr

$i_{juv} = 1.50$ (Gotshall 1969, 1972)

i_{larval} = instantaneous rate of larval mortality.

$$\text{Solving } i_{larval} = \frac{1.5(i) - 1.226(i_{juv})}{0.274}$$

Computed values of i_{larval}, along with overall larval survival (e^{-it}), from commercial catch sample estimates for 1961 to 1980 are shown in Table 2 and compared with our results for 1971 and 1972. Both sets of estimates indicated that 1971 was a very poor year for larval survival, while 1972 was slightly above average.

Factors Affecting Larval Survival

Comparison of onshore-offshore distribution patterns and wind patterns between 1971 and 1972 suggested that Bakun's upwelling index (1973, footnote 4) might be a useful indicator of habitat quality for survival of larval *P. jordani*. A study of possible correlations was originally made with data from 1961 to 1973. Fortnightly, monthly, and quarterly indices were calculated and regressed against the apparent overall larval-juvenile survival ($e^{-it} \times 10^4$). The July index was the most highly correlated for a single month ($R = 0.599$), while the average for the June through August period gave the highest correlation found ($R = 0.749$). For those months the equation

$$\text{Larval survival} = e^{-it} \times 10^4 = 0.73\ (\text{upwelling index}) - 8.31$$

accounted for 56.2% of variability in larval survival. A new equation based on data from 1961 through 1980,

$$\text{Larval survival} = e^{-it} \times 10^4 = 0.889\ (\text{upwelling index}) - 9.652,$$

accounts for 54.9% of the 20 yr variability in larval survival. The slope is significantly different from zero ($t_{18} = 4.81, P < 0.001$). The point for 1967 contributes strongly to the strength of the relationship, but the regression is significant without it ($t_{17} = 3.35$, $P < 0.01$). The relationship between larval survival and upwelling index is shown in Figure 15.

This relationship of survival to upwelling strength

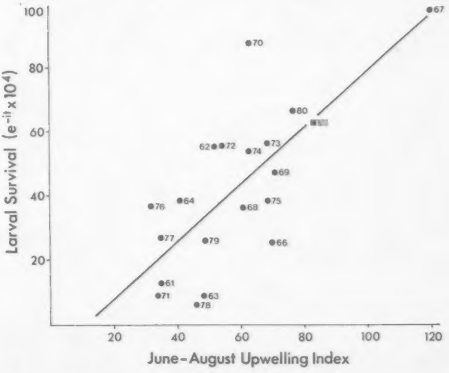


FIGURE 15.—Relationship between average upwelling in June through August 1961 to 1980 and estimated larval survival ($e^{-it} \times 10^4$) 1961 to 1980, with fitted regression line.

gives some insight into what factors may limit survival, and thus year class strength, in the *P. jordani* fishery. Surface seawater temperatures in 1971 and 1972 (Fig. 5) were different in several respects. The regression analysis draws attention to months from June through August. In these late months of larval development, temperatures were several degrees higher at nearshore stations in 1971 than in 1972. Evaluation of laboratory rearing experiments showed that survival was highest at 11° to 12°C, and it decreased rapidly above that range (Rothlisberg 1979).

DISCUSSION

Movements of adult *Pandalus jordani* associated with reproductive events have not been well defined. In contrast to other pandalids, e.g., *P. borealis* (Haynes and Wigley 1969; Horsted and Smidt 1956) and *P. montagui* (Lebour 1939, 1947; Mistakidis 1957; Allen 1963), there is no evidence of an inshore migration of female *P. jordani* prior to hatching of eggs they bear. Dahlstrom (1970) found that *P. jordani* at Morro Bay, Calif., moved 2 to 3 nmi farther offshore to spawn in the winter. Lukas and Hosie (1973) reported that female *P. jordani* left their study area 10 to 20 nmi off Tillamook Head, Oreg., in the fall. Numbers in March were greater at the south end of their grid than to the north, but there was no evidence of inshore or offshore movement associated with hatching. During the present study off Newport, Oreg., we found highest concentrations of adult *P. jordani* between 20 and 25 nmi offshore. While trawling was casual, and results are not reported here, there was no evidence of shoreward movement of ovigerous females during the period of hatching.

Prevailing wind and resultant currents could have transported larvae to the nearshore zone during the present study. Differences in wind and current between 1971 and 1972 are reflected in larval distributions for the two years. Furthermore, extended alongshore sampling in 1972 showed that shifts in distribution along the Newport line were representative of shifts along the whole coast. Shifts were not restricted to areas of high adult abundance.

Widespread distribution of early zoea in early and mid-March 1971 can probably be attributed to the mixed winds of February and to the spell of northwest wind in mid-March. More dramatic offshore displacement was seen in early May 1971, when larvae were found in abundance at 50 and 60 nmi. Numbers decreased markedly after May, probably through continued offshore displacement beyond the sampling area. More limited offshore displacement of early larvae in 1972 coincides with stronger, more consistent southwest winds in February and March of that year. Older larvae were generally closer to shore in 1972 than in 1971. Offshore displacement by upwelling probably was reduced in 1972 by the advanced larval development at the initiation of upwelling compared with 1971. Since older larvae live deeper in the water column (Rothlisberg and Pearcy 1977), late onset of upwelling with respect to the development sequence will produce less offshore displacement.

Year-to-year fluctuations in seasonal winds, upwelling, and surface advection in the northwest Pacific have been repeatedly described (e.g., Wickett 1967; Hubbard and Pearcy 1971; Peterson and Miller 1975). However, until the upwelling index was developed by Bakun (1973), it was difficult to correlate strength of upwelling in a long sequence of years with variations in productivity at any level. This now can be done, although specific processes involved may remain obscure. Several of the features of upwelling may act to change production of a given life stage or species. The correlation we found between upwelling index and larval survival is something of a surprise. Earlier studies (Winnor 1966; Wickett 1967; Hubbard and Pearcy 1971) stressed the advective nature of upwelling. Thus we expected greater larval "wastage" to seaward for years with early onset and greater strength of upwelling. The colder temperatures also might be supposed detrimental to *P. jordani* because they should slow development. The unexpected, high, positive correlation of larval survival and June to August upwelling can be explained by other knowledge of larval physiology in *P. jordani*. Laboratory rearing experiments have shown optimal larval survival at 11° to 12°C (Rothlisberg 1979). Upwelling maintains these relatively low temperatures through the summer months, whereas weaker upwelling allows summer warming (Patullo et al. 1969). Temperatures above 14°C in June 1971 would have been harmful and may have contributed directly to low larval survival in that year.

The reproductive strategy of *P. jordani* appears to rely on the complex advection of late winter and spring. Many demersal species of the Pacific northwest spawn in winter and spring, apparently to maximize onshore drift of larvae and retention in coastal nursery grounds (Parrish et al. 1981). *Pandalus jordani* larvae, on the other hand, hatch in late winter and have a planktonic phase extending through the transition from northward-onshore to southward-offshore currents. They should usually encounter 1) onshore retention in early stages and 2) offshore displacement of later stages during subse-

quent upwelling, reaching deeper water over habitat suitable to settling.

Application to all years uniformly of Gotshall's (1969, 1972) instantaneous mortality for juvenile *P. jordani* on the bottom ignores the certain variation in that mortality. Despite this limitation, the estimate of larval survival derived from the analysis was similar to estimates from our 2 yr of intensive plankton sampling. We are aware of the dangers of a comparison based on only two spawning seasons, but the comparison is in the correct direction, and it is all we have. Although there are limitations, comparison of egg numbers with numbers of first fishery recruits shows promise for identifying conditions critical in establishing year class strength. Higher resolution could be obtained if annual estimates of early benthic mortality were made, perhaps using the Pacific hake, *Merluccius productus*, as a biological sampler.

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EFFECTS OF BENZO(A)PYRENE ON THE EARLY DEVELOPMENT OF CALIFORNIA GRUNION, *LEURESTHES TENUIS* (PISCES, ATHERINIDAE)

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ABSTRACT

Benzo(a)pyrene (BaP), which is carcinogenic and mutagenic in mammals, exists worldwide in the marine environment. Sources of this polycyclic aromatic hydrocarbon include oil spills, industrial effluents, and atmospheric fallout. This study is the first to examine the effects of BaP on the embryonic development of a teleost, the California grunion. Gametes were stripped from spawning adults. and eggs were artificially fertilized. The fertilized eggs were then incubated for up to 14 days with initial concentrations of BaP ranging from 0 to 869 ppb. Steady-state tissue levels of BaP ranged from 0.46 to 19.92 ppm, which represented bioaccumulation factors of 146-437 times the steady-state BaP concentrations in seawater. When compared with controls, embryos exposed to initial BaP levels of 24 ppb or greater showed decreased hatchings, reduced notochord lengths, and increased morphological abnormalities. These results suggest that exposure of grunion embryos to BaP in contaminated areas may lead to their decreased survival.

Benzo(a)pyrene (BaP) is one oil constituent commonly found in marine sediments and organisms (ZoBell 1971; Neff 1979). This polycyclic aromatic hydrocarbon is introduced into the ocean via oil spillage, offshore drilling leaks, industrial effluents, runoff of asphalt roads, creosoted pilings, and atmospheric fallout (Andelman and Suess 1970; Dunn 1976; Puffer et al. 1979). Because BaP exhibits toxic, mutagenic, and carcinogenic properties in mammals, one might infer that it could also exert detrimental effects on fish populations (Heidelberger 1975; Miller 1978). Such effects could lead directly to a decrease in a valuable food source and pose a public health problem in the consumption of contaminated seafoods (Dunn and Fee 1979).

Awareness of significant BaP contamination in the marine biota has led to research on adult stages (Lee et al. 1972; Puffer et al. 1979) and, more recently, the sensitive embryonic-larval stages of fish (Hose et al. 1981, 1982). Grunion are particularly suitable for such a study because their embryonic development is well documented and they are easily reared in captivity (David 1939; Ehrlich and Farris 1971). Furthermore, grunion spawn on sandy beaches where developing eggs remain in the sand until the tide uncovers, agitates, and stimulates the eggs to hatch (Walker 1952). During this time, the developing eggs may be exposed to BaP. Therefore, we have undertaken this study to examine the effects of BaP on the early life history of California grunion, *Leuresthes tenuis*.

MATERIALS AND METHODS

Decontaminated seawater (sterilized, free of detectable BaP and particulate matter) was obtained by exposure of Los Angeles Harbor water to direct sunlight for 1 wk. Photooxidation by sunlight resulted in the breakdown of contaminating BaP to noncarcinogenic byproducts such as phenols and quinones (National Academy of Sciences 1972). Seawater exposed to sunlight was filtered through Whatman No. 5 filters to remove large, particulate matter and then sterilized by ultraviolet light. Water was maintained at a salinity of 31-32 ‰, a pH of 7.7-7.9, and a temperature of 20.0°-21.5°C.

BaP was dissolved in acetone, mixed with decontaminated seawater, and stirred for 24 h. The added concentrations of BaP in seawater were 5, 10, 100, 500, 1,000, and 5,000 ppb. The final concentration of acetone in the control and BaP-treated groups did not exceed 0.04%. Spawning California grunion were collected at Redondo Beach, Calif. Gametes were stripped and artificially fertilized in BaP-free, decon-

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taminated seawater. One hour after fertilization, three replicates of 25-35 eggs for each treatment level were placed in glass incubation jars (12.8 × 5.4 cm) which were wrapped with black tape and aerated with Pasteur pipettes connected to air pumps. Each jar contained 100 ml of decontaminated seawater to which various levels of BaP had been added as described above. In all cases, sand was excluded as an incubation medium. Dissolved BaP concentrations were measured when the California grunion eggs were introduced into the glass jars and on alternate days until day 15, using fluorescence spectroscopy (365 nm excitation, 405 nm emission) (Felton et al. 1982). Seawater samples (2 or 4 ml) were analyzed by Aminco-Bowman spectrophotofluorometer sensitive to 2 ng BaP.

Hatching and morphological abnormalities were observed and photographed at intervals over a 14-d period using a Wild M5 dissecting microscope and a Zeiss[5] photomicroscopy attachment. The significance of arc sin-transformed percentages of abnormalities was tested using analysis of variance followed by the Student-Newman-Keuls multiple range test (Sokal and Rohlf 1969). Notochord length of embryo and yolk-sac larvae was measured using a calibrated ocular micrometer. Notochord length was defined as the distance from the tip of the snout to the tip of the notochord before flexion and was always measured on the left side of the embryos and larvae. Deformed, circular-shaped embryos were measured from the posterior tip of the deformed notochord to the opposite side of the embryo, and this diameter was used to calculate the circumference which was considered to be equal to the notochord length. All values were recorded to the nearest 0.1 mm. Differences were tested using analyses of variance and the Student-Newman-Keuls test.

To measure accumulation of BaP by California grunion embryos, two additional series of incubation jars were prepared containing similar BaP concentrations and to which was added a small amount (6.7 nCi) of (α7, 10-^{14}C) benzo(a)pyrene (Amersham/Searle Corp., Arlington Heights, Ill.; 21.7 mCi/mmol, 99% chemical and radiochemical purity). On alternate days, three replicate samples of two eggs each were taken from the ^{14}C-BaP series to measure BaP accumulation using the method of Hose et al. (1981). Radioactivity was measured using a Beckman LS250 scintillation counter with an efficiency of 80% at 4°C. Total radioactivity was calculated using a series of solubilized embryos as the quenched standards.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

BaP Determinations

Added BaP levels of 5, 10, 100, 500, 1,000, and 5,000 ppb to seawater yielded initial BaP concentrations in the incubation jars of 4, 7, 24, 297, 361, and 869 ppb, respectively, when measured at time "0" when the California grunion eggs were introduced into the jars. Dissolved BaP levels declined thereafter with a half-life of 3.0±0.1 d ($\bar{x}$±SD) until steady-state levels of 24 ppb (361 ppb initial), 9 ppb (297 ppb initial), 5 ppb (24 ppb initial), 3 ppb (7 ppb initial), and 2 ppb (ppb initial) were reached within 4-10 d (Fig. 1). Stable BaP levels occurred most rapidly at lowest doses, while BaP concentrations in jars receiving the highest initial dose of 869 ppb decreased throughout the experimental period and did not achieve steady-state.

Accumulation of ^{14}C-BaP

The amount of BaP plus its metabolites in each egg corresponding to measured ^{14}C increased from day 1

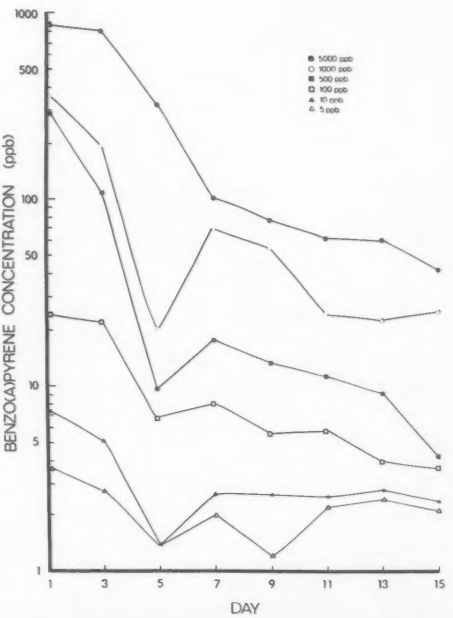


FIGURE 1.—Dissolved benzo(a)pyrene (BaP) concentrations following addition of 5-5,000 ppb BaP during the 14-d incubation period for the California grunion.

to day 3 in direct proportion to initial BaP concentrations and remained at steady-state levels thereafter for all groups except those exposed to an initial BaP dose of 297 ppb (Fig. 2). In embryos from this group, levels of BaP plus its metabolites increased throughout the exposure period ($R = 0.882$, 5 df, $P<0.01$). At day 15, BaP concentrations in treated embryos ranged from 0.459 (4 ppb initial) to 19.918 (869 ppb initial) ppm wet weight (Table 1). Tissue burdens from the initial BaP concentrations corresponded to bioaccumulation values of 127 to 23. Bioconcentration factors of 146-437 over steady-state BaP levels were measured.

Hatching

Hatching results are shown in Table 2. Low-level exposure to initial concentrations of BaP (4 and 7 ppb) had no significant effect ($P>0.05$) on the hatching abilities of exposed California grunion embryos, compared with the controls. However, with initial concentrations of 24 ppb and greater, significant differences ($P\leq0.05$) were observed between the control and experimental groups. At 24 ppb, 78% of the California grunion hatched, as compared with an average 95% hatching success in the controls. At 297 ppb only 6% of the California grunion hatched. After being exposed to 361 ppb BaP, only two of 95 larvae hatched, and both were abnormal. No eggs hatched after exposure to initial BaP concentrations of 869 ppb. Of those eggs which hatched on day 10, 99% had been exposed to 0 and 4 ppb initial BaP concentrations, 94% had been exposed to 7 ppb BaP, and 92% had been exposed to 24 ppb. All other hatchings occurred by day 13.

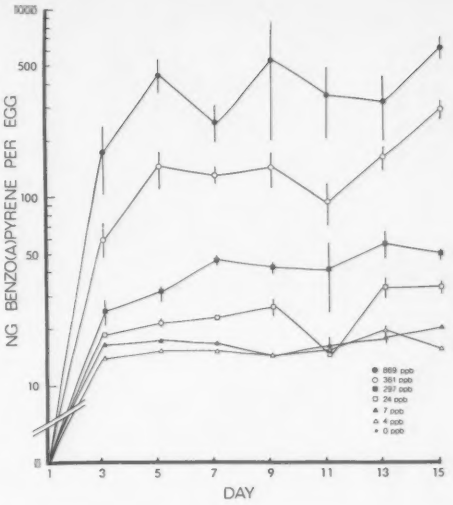


FIGURE 2.—Amount of benzo(a)pyrene (BaP) per California grunion egg corresponding to accumulated radioactivity (6.7 nCi ^{14}C-benzo(a)pyrene/ug BaP) during the 14-d incubation period. Initial dissolved BaP concentrations ranged from 0 to 869 ppb. Values shown are mean + standard deviation.

TABLE 1.—Tissue burdens of benzo(a)pyrene (BaP) and bioaccumulation factors in 15 d-old California grunion embryos.

Initial BaP concentration of seawater (ppb)	Embryo BaP concentration[1]		Bioconcentration factor	
	Wet weight (ppm)	Dry weight (ppm)	Initial BaP level in seawater	Steady-state BaP level in seawater
4	0.459±0.002	3.021±0.076	127±3	241±6
7	0.594±0.026	3.911±0.173	81±4	214±13
24	0.922±0.079	6.872±0.586	38±3	200±17
297	1.374±0.098	10.232±0.731	5±0	146±9
361	10.480±2.256	62.798±13.521	35±8	437±94
869	19.918±2.700	112.034±15.164	23±3	—[2]

[1] $\bar{x}$±SD, $n = 5$.
[2] Steady-state concentration not reached during study.

TABLE 2.—Percent hatching of California grunion eggs exposed to increasing BaP concentrations.

Initial BaP concentration (ppb)	Eggs		
	Total no.	No. hatched	% hatched[1]
0	88	84	95.4±5.5
4	87	81	93.3±2.8
7	92	83	90.3±11.2
24	84	65	78.1±8.2
297	81	5	6.2±6.0
361	95	2	2.1±1.8
869	90	0	0±0

[1] $\bar{x}$±SD, $n = 3$.

Abnormalities

There was significant difference ($P\leq0.05$) between percent of abnormalities in yolk-sac larvae in the control groups and those in groups exposed to initial BaP concentrations of 24 ppb or greater (Table 3). Of hatched larvae exposed to 24 ppb BaP, almost 20% were abnormal, over twice the number of abnormalities found in the control group. From solutions

TABLE 3.—Percent of California grunion yolk-sac larvae with developmental abnormalities when exposed to increasing concentrations of BaP.

Initial BaP concentrations (ppb)	Eggs hatched		
	No.	No. with developmental abnormalities	% with developmental abnormalities[1]
0	84	8	9.4±3.4 (3)
4	81	7	8.8±2.8 (3)
7	83	13	15.5±7.5 (3)
24	65	13	20.0±2.4 (3)
297	5	2	41.6±11.8 (2)[2]
361	2	2	100.0±0 (2)[2]
869	0	0	0

[1]±SD (*n*)
[2]No eggs hatched in one replicate of these series, therefore *n* = 2.

containing 297 ppb BaP, 42% of the yolk-sac larvae were abnormal.

Gross abnormalities observed in yolk-sac larvae exposed to 24 ppb BaP included lateral foldings of the posterior one-fourth of the tail, absence of caudal fin folds, and hemorrhagic lesions or congested vasculature in the caudal region (Table 4).

In contrast, development of embryos exposed to 24-361 ppb BaP for 14 d was retarded and resembled that of the normal embryo at 2.5 and 5.5 d of age (Fig. 3a, b) (David 1939). Abnormalities included 1) malformed tails with congested vessels or hemorrhage, 2) sporadic heartbeat resulting in intermittent blood flow, 3) head displacement in relation to the yolk sac, and 4) lack of melanophores near the lateral line above the intestinal tract.

Embryos exposed to 869 ppb BaP for 14 d resembled normal embryos at 1.2-2.5 d of age (David 1939). However, affected embryos had a lateral curvature midbody with occasional melanophores found on the trunk. In general, those embryos with shorter notochord lengths were observed to have yolk sacs much larger than those of the controls.

TABLE 4.—Abnormalities observed in California grunion yolk-sac larvae and embryos exposed to increasing concentrations of BaP.

	BaP exposure (ppb)	Abnormality
Yolk-sac larvae	24	Lateral folding of posterior fourth of tail. Absence of caudal finfold. Congested vasculature on caudal region.
Embryos	24-361	14-d-old embryo retarded in growth (resembled normal embryo growth at 1.5-5.5 d of age). Sporadic heart beat. Displacement of head in relation to yolk sac. Absence of melanophores near lateral lines. Absence of lens formation. Lesions as in larvae (above).
	869	14-d-old embryo retarded in growth (resembled normal embryo growth at 1.2-2.5 d of age). Lateral curvature midbody. Absence of melanophores (except in trunk region). Unused yolk sac. Lesions as in larvae (above).

Notochord Length

Notochord lengths (NL) of embryos and yolk-sac larvae are shown in Figure 4. Larvae which hatched after exposure to initial levels of BaP up to 361 ppb were not significantly different from controls in length ($P>0.05$). Shorter notochord lengths were observed in embryos exposed to BaP concentrations >7 ppb ($P<0.05$). Upon hatching, the mean notochord length of the control larval group was 5.8 mm, while embryos of the same age exposed to 24 ppb BaP averaged 4.0 mm NL.

DISCUSSION

Toxic and teratogenic effects of the carcinogen BaP on developing fish were studied by incubating embryonic stages of California grunion to increasing concentrations of BaP. Eggs were hatched in seawater alone, although California grunion eggs are normally incubated in sand. David (1939) concluded that there was probably no special adaptation of embryo metabolism to sand incubation, and speculated that spawning in the sand was a mechanism to protect eggs from predation. Incubation in seawater without sand permitted optimal observation of embryonic development with minimum disturbance. Also, exclusion of sand reduced the possibility of fungal and bacterial overgrowth and eliminated any possible contamination and influence by sand and/or sand-absorbed materials, as well as eliminating a large, potentially adsorptive surface for BaP. Preliminary trials resulted in a hatching rate of 90-100% in our laboratory, comparable to values previously reported (David 1939; Hubbs 1965).

Because of the low solubility of BaP in seawater, it was necessary to select a solubilizing or dispersing agent to create a uniform distribution (Davis et al. 1942; Wilk and Schwab 1968; Neff 1979). Such an agent could affect early development by acting in an additive or synergistic manner with BaP. Solvents examined in preliminary studies were benzene, Triton X-100, trioctanoin, and acetone, all of which caused observable alterations except for acetone in low concentrations. Triton X-100 and trioctanoin proved lethal, whereas the carcinogen benzene induced tail malformations. The validity of utilizing a solvent to distribute high levels of BaP in seawater can be compared with the not-uncommon situation in nature whereby lipophilic compounds are solubilized by contaminating substances such as detergents or oils. Also, certain solvents in which BaP is soluble, such as benzene, toluene, and xylene, are present in varying quantities in crude and refined oil. However,

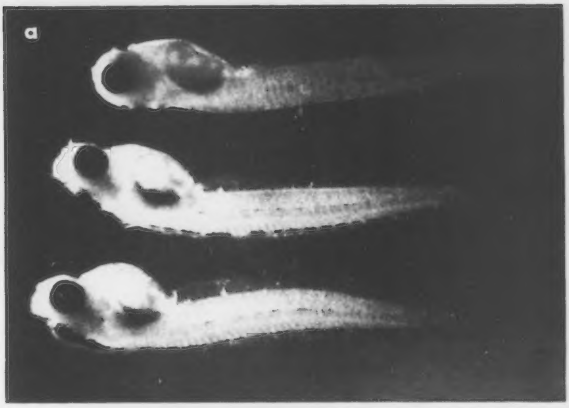
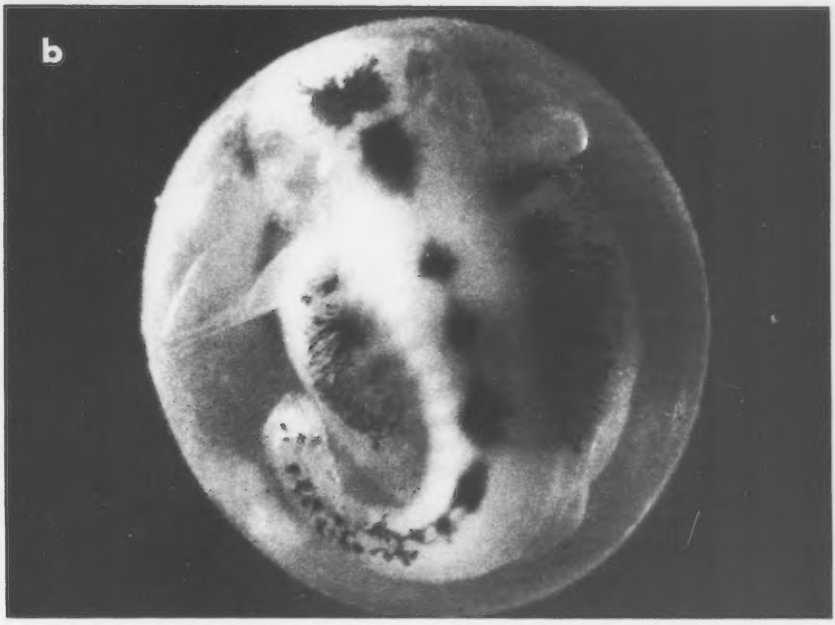


FIGURE 3.—California grunion incubated in decontaminated seawater, 14-d postfertilization: a) newly hatched larvae, with no benzo(a)pyrene (BaP) present (control) (90×); b) embryos, initially containing 24 ppb BaP (540×).



it should be emphasized that this study was not undertaken to duplicate field conditions of environmental exposure of California grunion eggs incubating in contaminated sands, although our results suggest that such studies are warranted.

Another difficulty was the decline of dissolved BaP over the 2-wk span in which the embryos were exposed (Fig. 1). This decline occurred despite precautions such as wrapping the jars to prevent photooxidation and opening the jars for daily inspection only under subdued light filtered free of ultraviolet wavelengths which degrade BaP. Loss of BaP could be caused, perhaps, by oxidation and adherence to glass, in addition to the uptake and metabolism of BaP by the embryos themselves. Felton et al. (1982) demonstrated that 16-20 ppb of crystalline BaP could be dissolved with agitation. This concentration could not be maintained,

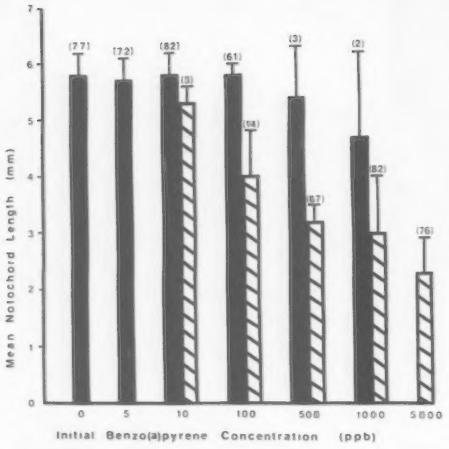


FIGURE 4.—Mean notochord length of California grunion embryos (slashed bars) and yolk-sac larvae (black bars) after 14-d incubation in seawater containing 0-5,000 ppb benzo(a)pyrene. Vertical lines = SD; numbers in parentheses = total no. embryos or larvae.

however, without continued addition of BaP; in fact, it decreased to about 1 ppb after several hours. Additional BaP dissolved in ethanol resulted in levels that decreased to near zero in 24 h. Struhsaker (1977) reported a similar difficulty in maintaining a stable concentration of benzene in seawater and attributed this to the volatility of benzene.

Because the uptake of polycyclic aromatic hydrocarbons occurs primarily via the aqueous BaP fraction, rather than by direct accumulation from surrounding sediment (Roesijadi et al. 1978), the exposure of grunion eggs to BaP in these experiments may simulate what occurs in the natural environment. For example, an oil spill may result in initially high concentrations of hydrocarbons, but photooxidation, adsorption into sediments and water-column particulates, and tidal action will decrease the concentrations of various oil constituents (such as BaP) over time. We have periodically monitored unfiltered waters of the Los Angeles Harbor for BaP concentration during the period 1977-81. Levels of BaP fluctuated from below the limit of detectability (<0.1 ppb) up to 5.4 ppb (Puffer et al. 1979). Niaussat and Auger (1970) have reported levels of 1.6 ppb BaP in seawater collected from a remote, isolated atoll in the eastern tropical Pacific Ocean. BaP levels in sand collected offshore of Cabrillo Beach in the Los Angeles Harbor ranged from 223 to 471 ppb (Duncan and Puffer 1982) and as high as 18,000 ppb in sediments from the inner Los Angeles Harbor (Gossett et al. 1983). Concentrations of BaP in sediments worldwide have ranged from nondetectable levels up to 15,000 ppb (Neff 1979). This suggests that embryos may be exposed to high levels of BaP in interstitial water during incubation in sand. As there were no prior studies regarding the effect of BaP on early grunion development, we utilized a wide range of BaP concentrations to achieve various tissue burdens. This not only reflects the broad range of exposure in nature, but also affords an opportunity to assess the sensitivity of eggs incubated under controlled conditions in seawater containing various concentrations of BaP and to correlate observed effects with known tissue BaP levels in embryos.

The extent of BaP uptake by California grunion embryos was directly proportional to initial and steady-state BaP concentration in seawater. By day 15, embryos accumulated BaP at levels 146-437 times the steady-state BaP concentration in seawater.

Comparative BaP bioaccumulation factors range from 5,142 to 21,000 for rainbow trout alevins and flatfish larvae, respectively (Hose et al. 1981; Hannah et al. 1982) and 861 for the clam *Macoma inquinata* (Roesijadi et al. 1978). While Hannah et al. (1982) noted an increase over time in BaP concentrations in embryonic rainbow trout, tissue BaP levels in California grunion remained essentially constant from day 3 to day 15. Eldridge et al. (1978) demonstrated that tissue levels of benzene in Pacific herring, *Clupea harengus pallasii*, reached equilibrium within 6-12 h at 11 times the initial water concentration. Steady-state tissue levels of BaP probably represent an equilibrium between pollutant absorption, embryonic metabolism, and excretion of the more hydrophilic metabolites (Binder and Stegeman 1980).

The observed alterations in development of California grunion exposed to BaP include 1) hatching, 2) abnormalities, and 3) reduction of notochord length. The earliest consequence of egg exposure to BaP was a reduction in hatching rate. Initial concentrations of BaP >24 ppb caused a significant mortality of yolk-sac larvae. These results are consistent with those reported by Ernst et al. (1977) who showed a 25/25 (100%) hatching rate of *Fundulus grandis* eggs exposed to 1.1 ppm water-soluble fraction of No. 2 fuel oil, a 4/25 (16%) hatching rate when exposed to 2.2 ppm, and 0/25 (0%) when exposed to 4.4 ppm. BaP has long been known to be embryo toxic in rodents (Rigdon and Rennels 1964) and more recently in sand sole, *Psettichthys melanostictus*, (Hose et al. 1982) and following maternal exposure in flathead sole, *Hippoglossoides elassodon*, (Hose et al. 1981). Furthermore, petroleum hydrocarbons, including

BaP, can alter the duration and time of teleost hatching (Ernst et al. 1977; Leung and Bulkley 1979; Hannah et al. 1982). Normally, hatching of California grunion eggs occurs in 10-14 d. Since most hatched eggs in this study did so on day 10 and no later than day 13, no effect was noted on duration and time of hatching of California grunion eggs. The dramatic and significant effect was on hatching rate.

The second effect noted was increased abnormalities of the developing yolk-sac larvae embryos. Of those yolk-sac larvae observed, 20% had a midbody lateral curvature when exposed to 24 ppb BaP or greater, as compared with 9% of the controls. Vascular abnormalities observed in embryos included stasis in yolk-sac vessels, apparent hemorrhages in the caudal regions, intermittant heart beat, and distinctly underdeveloped bodies with nonutilized yolk hydrocarbons (Ernst et al. 1977; Lonning 1977), particularly BaP (Hose et al. 1981, 1982; Hannah et al. 1982). Depressed heart rates of fish embryos treated with high levels of petroleum hydrocarbons have been attributed to inhibition of metabolism and/or neurotransmission (Whipple et al. 1981) and can result in partial or complete mortality (Anderson et al. 1977).

The third response observed in California grunion embryos exposed to BaP was reduction in notochord length. The notochord length of embryos exposed to 24 ppb BaP averaged 70% of that of controls. At 297 ppb BaP or greater, the notochord length of affected embryos was generally <50% of the notochord length of the control group. Retarded growth was also evident in rainbow trout alevins reared in 0.08-2.99 ppb BaP (Hannah et al. 1982) and may result from the inhibitory effects of polycyclic aromatic hydrocarbons on DNA synthesis (Santodonato et al. 1981) and, hence, mitosis (Bourne and Jones 1973; Kocan et al. 1981).

At the end of 14 d, embryos exposed to initial concentrations of 24-297 ppb BaP resembled normal embryos at 2.5-5.5 d of development. This retarded growth was characterized by a lack of lens formation, absence of caudal fin folds, and a reduced number of melanophores. However, there was one exception to this trend of slow development: The pectoral fins of embryos treated with 24-297 ppb BaP appeared to be of normal size and maturity, whereas all other aspects of embryo development seemed severely delayed. Irregular cleavage and retarded development in oil-treated fish embryos have been previously described (Lonning 1977), and assessment of the developmental effects of petroleum hydrocarbons on marine fish eggs has been reviewed by Kuhnhold (1977). These include sublethal effects such as chromosomal aberrations and morphological anomalies as well as direct toxicity (Rosenthal and Alderdice 1976). Toxic hydrocarbon levels reportedly correlated with mitotic errors in eggs of Atlantic mackerel, *Scomber scombrus*, (Longwell and Hughes 1980). Anderson et al. (1977) also noted lack of pigmentation in estuarine killifish, and a histological examination of *Fundulus grandis* embryos exposed to the water-soluble fraction of No. 2 fuel oil revealed pathological lens, liver, kidney, and epthelial tissues (Ernst et al. 1977).

In summary, the effects observed in California grunion embryos exposed to the carcinogen BaP were threefold: Decreased hatching rates, increased number of morphological abnormalities, and shortened notochord lengths. These grossly visible alterations would be detrimental to the potential growth and survival of fish in the wild (Rosenthal and Alderdice 1976). The number of fish reaching adulthood would decrease directly as a result of the lethal effects of BaP on embryos and indirectly as a result of decreased ability of affected fish to elude predators. Also, short-term observations such as these do not address the problem of carcinogenesis, although recent experiments have demonstrated that the polycyclic aromatic hydrocarbon, 7,12-dimethylbenz(a)anthracene, is tumorigenic in freshwater fish (Schultz and Schultz 1982).

It is predicted that BaP will increase in the environment unless restrictions can be imposed upon its production. However, reduced production of BaP is unlikely, as this compound is an unavoidable by-product of incomplete combustion and petroleum usage (National Academy of Sciences 1972). Therefore, the results of our experiments indicate that the short- and long-term effects of BaP on the developmental stages of fish and other marine life warrant further investigation.

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SIMULATION OF THE NORTH ATLANTIC OCEAN DRIFT OF *ANGUILLA* LEPTOCEPHALI

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ABSTRACT

A numerical simulation model of surface current drift was developed in order to simulate the poorly understood drift migration of *Anguilla* leptocephali in the North Atlantic Ocean. The model was based upon the advection-diffusion equation, which was approximated by finite differences. Currents for the model were calculated from ships' drift data. Leptocephali were "started" at various points in the presumed American and European eel spawning areas, and the model produced spatiotemporal patterns of leptocephalus concentrations resulting from surface current drift and turbulent diffusion. In the American eel drift simulations the patterns followed a sequence of four phases: 1) Initial northwest drift on the presumed Antilles Current; 2) the formation of a "patch" of leptocephali offshore of Florida and the Gulf Stream; 3) dispersal along the North American coast resulting from the continued input of larvae into the Gulf Stream from the patch; and 4) transport eastward into the Atlantic on the Gulf Stream. In the European eel drift simulation, the leptocephali slowly spread throughout the Sargasso Sea region of the North Atlantic, and there was little Gulf Stream transport by the eighth month of drift. The patterns of distribution produced by the model correspond well with the limited collection data for both species, though it remains for future sampling efforts to verify whether the features present in the simulations actually occur.

Schmidt (1925) summarized over two decades of work to provide what has since become known as the "classical solution" to the Atlantic eel problem. Schmidt proposed that adult European eels, *Anguilla anguilla*, and American eels, *A. rostrata*, migrate in the fall from their freshwater habitats and travel to spawning areas in the Sargasso Sea. The adults spawn in the early months of the year and then die. The resulting larvae (termed leptocephali) are presumed to drift passively on surface currents toward their respective coasts. Schmidt stated that American eels, having a shorter distance to traverse, drift about a year as leptocephali before metamorphosing to the glass eel phase and commencing their migration toward freshwater. European eel leptocephali are presumed to take 3 yr to complete their journey. This scenario was challenged by Tucker (1959), who hypothesized that the two Atlantic anguillid eel species are in fact only one. Tucker proposed that all adult European eels die during their migration, that all anguillid leptocephali are the progeny of eels originating in North America, and that European eel stocks are replenished by leptocephali that simply drifted across the Atlantic after failing to land on the North American coast. Tucker felt that differences in the vertebral counts used to discriminate between the two species could be explained by a thermal shock suffered by developing embryos in part of the spawning area. Tucker's hypothesis has been largely discounted, and recent electrophoretic (Jamieson and Turner 1980; Comparini and Rodino 1980) and karyotypic (Passakas 1981) evidences indicate the existence of two anguillid eel species in the North Atlantic and associated freshwaters.

Nonetheless, there are persistent unanswered questions concerning the migrations of larval, juvenile, and adult eels (Vladykov 1964; McCleave and Harden-Jones 1979). One of these questions concerns the location and timing of American and European eel spawning. Schmidt (1925) identified the European eel spawning area as lying between lat. 22° to 30°N and long. 48° to 65°W, and stated that spawning "commences in late winter or early spring and lasts well on in summer." He based these limits on the distribution of the smallest leptocephali (<10 mm) he collected. To the present time no adult eel has been captured away from the continental shelves, and no identified anguillid eel eggs have been collected. Schmidt did not collect many small American eel leptocephali, and consequently his delineation of the American eel spawning area and time is much less precise. Recently there have been several systematic sampling efforts for small leptocephali with the ob-

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jective of defining the spawning areas of the European eel (Tesch et al. 1979; Schoth and Tesch 1981) and the American eel (McCleave and Kleckner[3]). Kleckner and McCleave[4] have obtained evidence that recently hatched American eel leptocephali are associated with a thermal front in the Sargasso Sea.

Also, little is known regarding the time course of the leptocephalus drift migration. Following Schmidt's (1925) summary, several authors have compiled information on the spatiotemporal distribution of anguillid leptocephali, including Smith (1968), Vladykov and March (1975), Tesch (1980), and Kleckner and McCleave (1980). These studies only provide a broad outline of the course of the leptocephalus drift migration, as the number of identified leptocephali collected is still small, considering the scale of the migration in terms of distance and probable numbers. The available data are difficult to interpret and may better represent the distribution of sampling effort than the distribution of leptocephali (Kleckner and McCleave 1980). Unless sampling at a particular location was done systematically, the absence of leptocephali from collections can only be interpreted as negative evidence concerning the presence of leptocephali at that location. It is still not known how leptocephali are transported in the Florida Current-Gulf Stream system. How do American eel leptocephali cross the Gulf Stream to approach the North American coast, and why are substantial numbers of these leptocephali not transported across the Atlantic to populate Europe? Are any behavioral components necessary in the leptocephalus drift migration? In summary, where and when are leptocephali most likely to be found, and what implications does this distribution have for the eel's life history and migration patterns?

To answer some of these questions a simulation model of leptocephali drift in the North Atlantic surface currents was developed. The intent was to implement the simulation so that leptocephali started at points in the presumed Sargasso Sea spawning area would be transported in a way realistically approximating actual surface current transport. The objectives of the research were to generate patterns of distribution representing the likely time course of a passive drift migration and to compare and interpret these distributional patterns with information about the actual leptocephalus distribution and the eel's life history. In this way the model serves an explanatory role, highlighting the factors important in generating a distribution of leptocephali, and also provides a framework for future research on the leptocephalus drift migration. Distributional patterns that developed during some of the simulations are presented here, with emphasis on the American eel; limited results for the European eel are also given.

[3]J. D. McCleave, Professor of Zoology, and R. C. Kleckner, Research Associate in Zoology, Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469, pers. commun. July 1981.

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MATERIALS AND METHODS

Anguilla leptocephali are found in the top few hundred meters of the water column (Kleckner and McCleave 1980; Schoth and Tesch 1981), and therefore the model was developed with only two horizontal spatial dimensions. The model was based upon the time-dependent, two dimensional form of the advection-diffusion equation:

$$\frac{\partial P}{\partial t} + \frac{\partial}{\partial x}\left(uP - K_x \frac{\partial P}{\partial x}\right) + \frac{\partial}{\partial y}\left(vP - K_y \frac{\partial P}{\partial y}\right) = 0$$

where P = concentration of leptocephali;
u and v = velocities in the respective x and y directions; and
K_x and K_y = diffusivity coefficients for the respective directions.

Leptocephali were not assumed to have any directed swimming capability, so the velocities in the above equation represent simple water current velocities. The diffusivity coefficients express the dispersion of leptocephali by turbulence, eddies, and other phenomena not expressed by the advective terms (Okubo 1980).

The derivatives in the above continuous equation were approximated by finite differences. For example, to approximate the time derivative the following relation was used:

$$\frac{\partial P}{\partial t} \cong \frac{P^{t+1} - P^t}{\Delta t}$$

where P^t = concentration of leptocephali at the present time t;
P^{t+1} = concentration of leptocephali at time $t + \Delta t$; and
Δt = duration of the time step.

The derivatives with respect to the x and y directions were approximated by weighted finite differences. The method developed by Fiadeiro and Veronis

(1977) was followed for determining the weighting so as to provide increased numerical stability and to approximate more closely the solution to the continuous equation. Further details on the numerical methods used were presented elsewhere (Power 1982).

In approximating the advection-diffusion equation by finite differences, the region under study is partitioned by a grid, and a difference equation is derived for each cell formed by the grid. The difference equations express the concentration of the substance at the center of each cell formed by the grid in terms of fluxes between adjoining cells. The end result is a large system of simultaneous (difference) equations, which can be repeatedly solved to obtain the cell concentrations at successive time steps. The region included in this study was the Gulf of Mexico, Caribbean Sea, and the North Atlantic Ocean between lat. 10° and 50°N and west of long. 40°W (Fig. 1). Coastlines were approximated by cell boundaries, as were the Caribbean islands and shoal waters of the Bahamas. Flux of leptocephali across these boundaries was prohibited. Leptocephali approaching the Bay of Fundy, Gulf of St. Lawrence, and the long. 40°W boundary of the model were permitted to be transported out of the modeled area (dashed lines in Figures 2-9).

Currents for the model were calculated using ships' drift data obtained from the National Oceanographic Data Center (Fig. 2). A ship's drift observation is the inferred surface current calculated by comparing the ship's true position after a given period of steaming with the navigator's dead reckoning position. Surface current charts of the North Atlantic are derived from the same data base used in this study. Each ship's drift observation was resolved into an east and north component, and the current component at the interface between two cells was calculated as the mean of all the appropriate current components recorded in the 1° of latitude and longitude bisected by the cell interface. The means were calculated by calendar months, so for each month in the simulations a different current regime was used. Using June as a representative month, the median number of observations used to calculate a current component was 10, and 75% of the components were calculated using five or more observations. The number of observations was greatest within 5° of the North American coast, with sample sizes >100 commonly occurring. Sample sizes were poorest in the southeast portion of the modeled area. An average of 3% of the cell interfaces had no associated ships' drift observations. These points where data were completely missing were

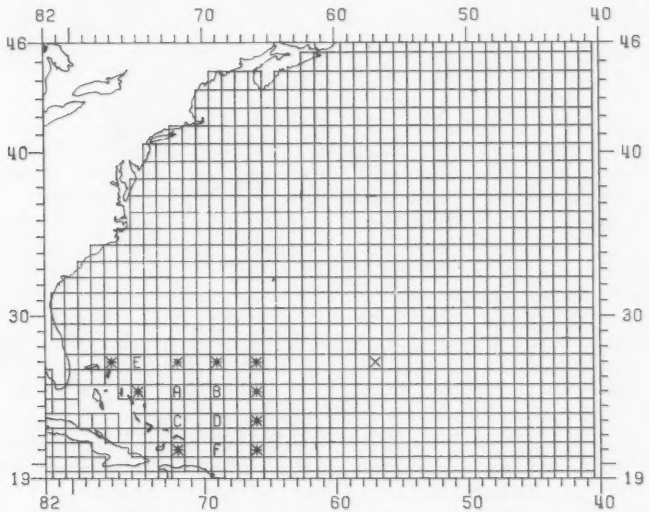

FIGURE 1.—Main portion of the geographic region included in the simulations, along with the 1° by 1° grid and coastline approximation. Lettered cells are the starting points for American eel leptocephalus drift simulations discussed in the text, and cells with stars are the starting points in other simulations not presented here. Note for comparative purposes that points A and C and points B, D, and F are the same meridians, while points A and B and points C and D share the same latitudes. Cell with an × is the starting point for the European eel drift simulation.

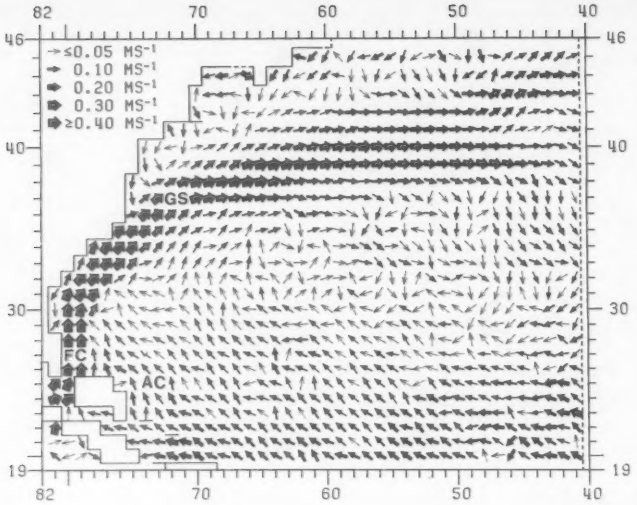

FIGURE 2.—Surface current vectors used in the simulations for the month of May. Vector in a cell was computed by taking the mean of the current components at the cell's edges and calculating the resultant vector. Key depicts representative current speeds. AC = Antilles Current; FC = Florida Current; GS = Gulf Stream.

irregularly spaced throughout the modeled area, so their components were calculated by interpolating between adjoining cells and months. Current velocities were necessarily taken as representative of the currents that occur throughout the depth range of *Anguilla* leptocephali. The leptocephali were assumed to maintain themselves continually in surface waters, so the finite differences were derived with no assumptions regarding fluid continuity. The effect of this is that leptocephali are concentrated in regions of net water convergence (downwelling) and dispersed from regions of divergence (upwelling).

The diffusivity coefficient (K) was calculated as a function of grid spacing. Data from numerous dye diffusion experiments reviewed by Okubo (1971) were used in a least squares regression analysis to compute the equation $K = (3 \times 10^{-4}) h^{1.1}$ relating the diffusivity parameter (in m^2/s) to the length scale (grid spacing) h in meters. No spatial variation in diffusivity, other than that due to meridional grid narrowing in more northerly latitudes, was assumed. Diffusivities used ranged from 68 to 110 m^2/s.

In carrying out the simulations, American eel leptocephali were considered to be "spawned" as point sources at the various locations designated by letters or stars in Figure 1. These starting locations cover most of the presumed geographic range of American eel spawning (Kleckner and McCleave 1980; Kleckner[5]). Locations designated by letters are in the area which, on the basis of collections of very small leptocephali, represent the principal spawning area. The distributional patterns of leptocephali started at these lettered locations are discussed in detail in this paper, and the various simulation runs are referred to by these letters. The date 1 March is representative of the peak American eel spawning period (Kleckner and McCleave 1980; Kleckner footnote 5). That point in time was used as the starting date for the American eel drift simulations, with no additional input of leptocephali after that date. The center of the estimated European eel spawning area (Schmidt 1925; Schoth and Tesch 1981) is marked in Figure 1 with an × at lat. 27°N, long. 57°W. The results of one simulation, in which leptocephali were started on 15 April at this point, are presented. The length of the time step in the simulations varied by month, but was always between 1.5 and 2.0 d. The simulation results are presented initially on a monthly basis and then later on a bimonthly basis.

There is little information regarding actual concentrations of leptocephali in the ocean. As the simulations progressed, individual cell concentrations were expressed as proportions of the start-

[5]R. C. Kleckner, Research Associate in Zoology, Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469, pers. commun. July 1981.

ing concentration. No mortality of leptocephali was incorporated into the model, and the total number of leptocephali was conserved throughout the simulation except for the portion transported across the open boundaries discussed previously. A unitless number is given when referring to a concentration, so that reference to a concentration of 10^{-3} refers to a concentration of leptocephali that is three orders of magnitude below the starting concentration. The concentration contours presented in Figures 3-9 were determined by linearly interpolating between the concentrations at the centers of the cells. Each contour represents an order of magnitude change in concentration relative to neighboring contours. Only leptocephalus concentrations $>10^{-7}$ (proportion of the starting concentration) are shown. In Figures 3-9 the leptocephalus starting location is marked by a star.

The choice of contour intervals as orders of magnitude was arbitrary; in some cases, the display masked the spatial structure of the distributions. This can occur where the order of magnitude contours are widely spaced, and a discontinuity in the concentrations is between the contours. For this reason an agglomerative cluster analysis using a spatial autocorrelation coefficient, Moran's I (Cliff and Ord 1973), as the metric was carried out with cell concentrations as the variable. The weighting coefficient was the reciprocal of the distance between cells, and only immediately adjacent cells were linked (rook's moves). Examination of the equation for Moran's I indicates that when choosing among several coefficient values, the minimum I represents the most spatially uniform distribution. The clustering proceeded iteratively by examining all possible pairwise linkages of clusters of cells, and forming a new cluster from the pair that yielded the minimum value of I for the new cluster. Thus at any stage the clusters partition the distribution into "patches," i.e., regions in which the cells are most spatially uniform in concentration. The cell concentrations were logarithmically transformed for the analysis to minimize the effects of outliers on I. The results of these analyses are not explicitly presented, but are referred to when necessary to facilitate the interpretation of the contour plots.

RESULTS

Distribution of Leptocephali After 30 Days of Drift

The proximity of the starting point to the Gulf Stream, the Antilles Current northeast of the Bahamas, and the Bahamas themselves all influenced the distributional patterns of American eel leptocephali that developed 1 mo after the 1 March starting date (Fig. 3). Capture of leptocephali by the Gulf Stream was already evident, and larvae started east and northeast of the Bahamas showed northwesterly drift on the Antilles Current.

Leptocephali begun at F mostly moved away from that location during the first month (Fig. 3F). The larvae were somewhat dispersed even at this early date, as cluster analysis indicated a large patch east of the Bahamas between lat. 21° and 26°N. Concentrations declined sharply to the east and south, as they did in all runs, indicating little transport in those directions. To the west, leptocephali were split by the Bahamas, approaching the Gulf Stream by both the route north of the islands and through the channel between the Bahamas and Cuba. Some passed completely through this channel to be caught in the Florida Current and carried northward, so that the 10^{-7} contour extended to lat. 32°N.

There was gradual northwesterly dispersal of leptocephali started at more northerly (Fig. 3B, D) and northwesterly (Fig. 3A, C) locations than those at F. The larvae in these runs are more concentrated, with most remaining near the starting points. In runs A-D larvae are impinging upon the Bahamas, and in C the concentrations offshore of the Bahamas are particularly high. This is due to the clearly evident Antilles Current transport in run C, and this current also facilitated the entry of run C larvae into the Gulf Stream. Runs A and E also show Gulf Stream transport, but this is more by virtue of their starting point's proximity to the Gulf Stream. Gulf Stream transport is pronounced in E, with the 10^{-7} contour reaching north to lat. 39°N and east to long. 65°W.

Distribution of Leptocephali After 60 Days of Drift

By 30 April, 2 mo after the 1 March start, leptocephali had spread and most moved northwest of their starting locations (Fig. 4). There were now broader areas of more moderate concentration, typified by the area enclosed by the 10^{-2} contour east of the Bahamas. Gulf Stream transport was now evident in all runs A through F.

Run F is notable for the substantial distance traversed by the larvae, considering the position of point F (Fig. 4F). This was primarily caused by continued transport between the Bahamas and Cuba, entry into the Florida Current, and then rapid Gulf Stream transport. Antilles Current transport also contributed. Concentrations in run F fell into three

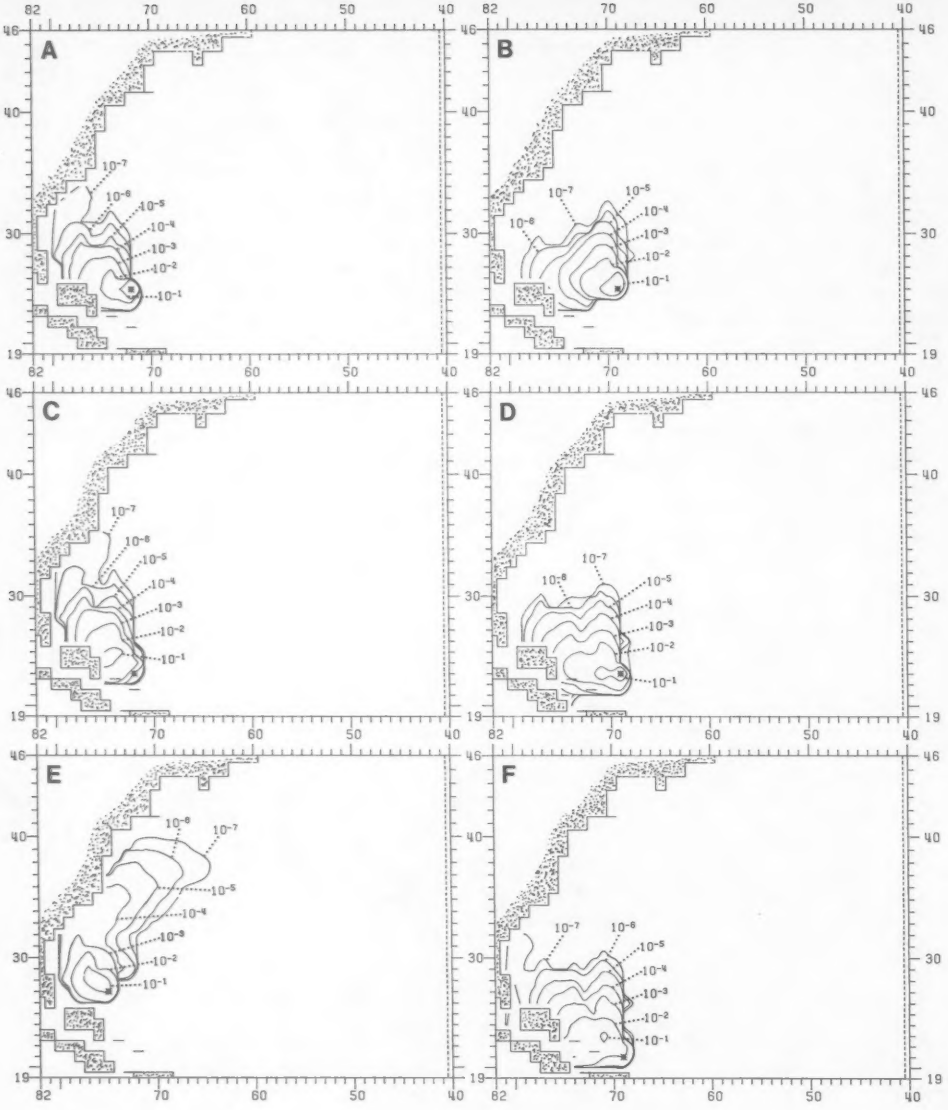

FIGURE 3.—Concentration contours of American eel leptocephali, expressed as a proportion of the starting concentration, for 30 March. Each lettered plot corresponds to the same lettered starting location in Figure 1. In this and subsequent figures stars mark the starting points. 30 March is 1 mo after the 1 March starting date.

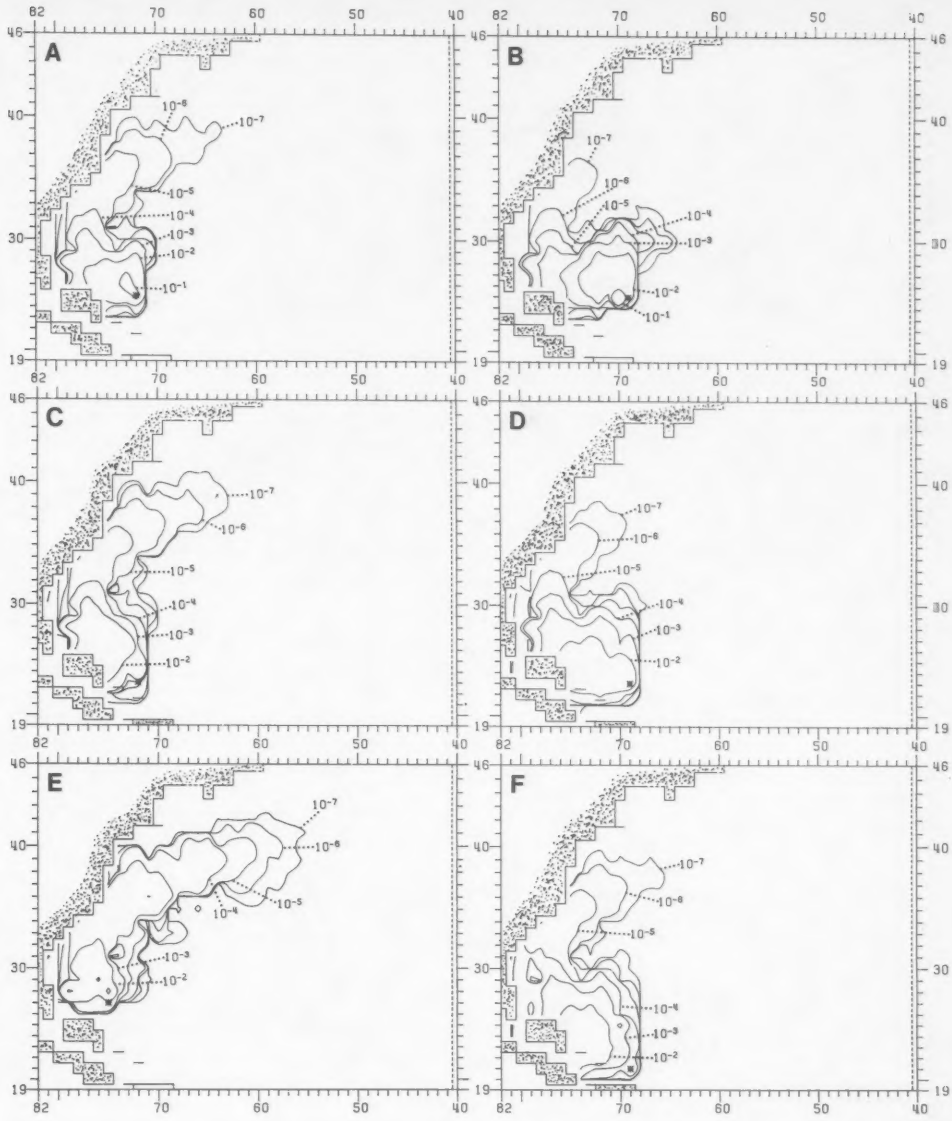

FIGURE 4.—Concentration contours after 60 d of American eel leptocephalus drift. Corresponding date is 30 April.

groupings: 1) High concentrations east of the Bahamas containing most leptocephali, 2) lower concentrations flanking this patch, and 3) Gulf Stream larvae.

Leptocephali started north and northwest of F (runs A through D) showed more uniform distributions than the previous month, although the sharp eastern and southern gradients were maintained. There was transport between the Bahamas and Cuba only in run D, and leptocephali in run B showed lesser dispersal when compared with other runs. Run C again showed most clearly the effects of Antilles Current transport, while run A showed a similar but less developed pattern. Leptocephali in runs A and C reached lat. 39°N and long. 65°W at concentrations $>10^{-7}$.

Run E continued to show the most widespread distribution, and while offshore of Florida there were still concentrations $>10^{-2}$, the 10^{-3} contour enclosed a considerable area offshore of the mid-Atlantic coast.

Distribution of Leptocephali After 90 Days of Drift

Runs A, C, D, and F became similar by the third month of drift (Fig. 5; 30 May). The cluster analyses for these simulations at day 90 are of interest, because in each a distinct geographic grouping of cells emerged consistently. These clusters did not combine with others until forced to do so at the final stages of clustering. This indicated that the cell groupings represented by the clusters had spatial distributions of leptocephali (as measured by Moran's I) which were internally more uniform than if cells external to the groupings had been included during clustering. This characterized (independently of concentration contour plots) an inportant feature in the spatial structure of the leptocephali at day 90. The clusters of cells in runs A, C, D, and F formed patches east of Florida and the Gulf Stream, north to northwest of the Bahamas, and northwest of the starting points (roughly between lat. 24° to 28°N and long. 71° to 77°W). These patches had mean cell concentrations of 0.015 to 0.025, and patch limits were approximated by the 10^{-2} contours (Fig. 5). The bulk of the starting concentrations was contained within these patches.

Another feature common to the A, D, and F runs was the large area of concentrations between 10^{-3} and 10^{-4} that paralleled the mid-Atlantic coast and then extended offshore at about lat. 38°N. Run C had an identical pattern, except that its concentrations in this area were an order of magnitude higher. This difference can be attributed to starting point C's location and the enhanced Antilles Current-Gulf Stream transport mentioned earlier.

Run B's pattern was similar to that of runs A, C, D, and F, but was not as fully developed. This is because run B leptocephali were started farther into the Sargasso Sea, where currents are weaker. The main patch of concentration was present, but it covered a broader area and had a slightly lower mean concentration of 0.01. The 10^{-5} contour along the North American coast in run B took the place of the 10^{-4} contour in runs A, D, and F. In B there were still high concentrations near the starting point.

Run E continued to exhibit the most extensive pattern of leptocephalus distribution (Fig. 5E). There was a patch offshore of Florida and the Gulf Stream with a mean cell concentration of 0.012, but it was smaller and farther north than the corresponding patch in other runs. More than half of the starting concentration lay north of lat. 31°N and within the 10^{-3} contour. Concentrations $>10^{-2}$ were well north of lat. 32°N in run E.

Distribution of Leptocephali After 150 Days of Drift

The patterns of distribution below lat 32°N persisted during the next several months in the simulations, while to the north there was an increase in the concentrations and continued Gulf Stream transport. The main patches of concentration offshore of the Gulf Stream and Florida remained in runs A, C, D, and F after 5 mo of drift (Fig. 6; 29 July). The patches moved slightly to the northwest, and lay between lat. 25° to 30°N and long. 70° to 78°W. This region still contained more than half of the total starting concentration in runs A, C, D, and F, and the mean cell concentration in this area was about 0.005.

The broad bands of concentration along the mid-Atlantic coast also persisted and increased in concentration to between 10^{-3} and 10^{-2}. This was a consequence of the patches offshore of Florida just mentioned. It appears the patches slowly introduced larvae into the Gulf Stream system. The subsequent transport in the Gulf Stream quickly spread larvae parallel to the coast, then offshore and out into the Atlantic. The patches in simulations A, C, D, and F formed in the same general location, so that for larvae carried north of lat. 30°N the starting location had a lesser effect on the distribution. This is illustrated by the fact that the 10^{-3} contours are virtually identical in position north of lat. 30°N in runs A, D, and F at 5 mo after starting. Run C formed the patch earlier, so more larvae had entered the Gulf Stream and were therefore more widely dispersed. Leptocephali at

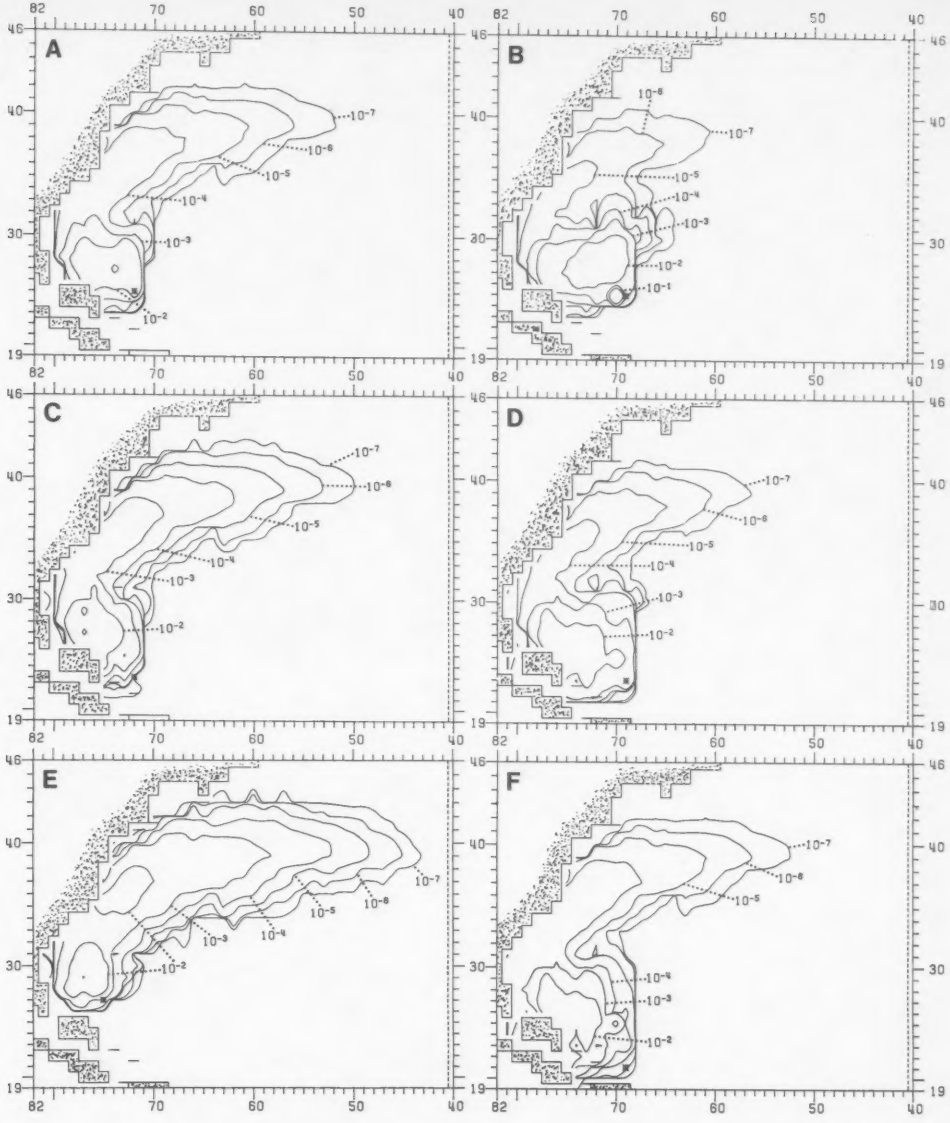

FIGURE 5.—Concentration contours of American eel leptocephali after 90 d of drift (30 May).

concentrations $>10^{-7}$ were now being advected past the long. 40°W border of the modeled area.

Run B's pattern at 5 mo was similar to those just discussed, but the main concentration of leptocephali was farther offshore of Florida and more broadly distributed (Fig. 6B) because the larvae were started in a region of weaker currents. There was a greater degree of northward transport from the main concentration, so that leptocephali joined the Gulf Stream at higher latitudes than in other runs.

The very large area enclosed by the 10^{-3} contour was the striking aspect of the pattern for run E at 5 mo (Fig. 6E). Cells in this area had a mean concentration of 0.002 and contained in total a concentration of 0.9. This region formed an exaggerated example of the results of prolonged leptocephalus entry into the Gulf Stream. In this case, the observed distribution is because larvae began close to the Gulf Stream, in the region where the main patch of concentration formed in other runs.

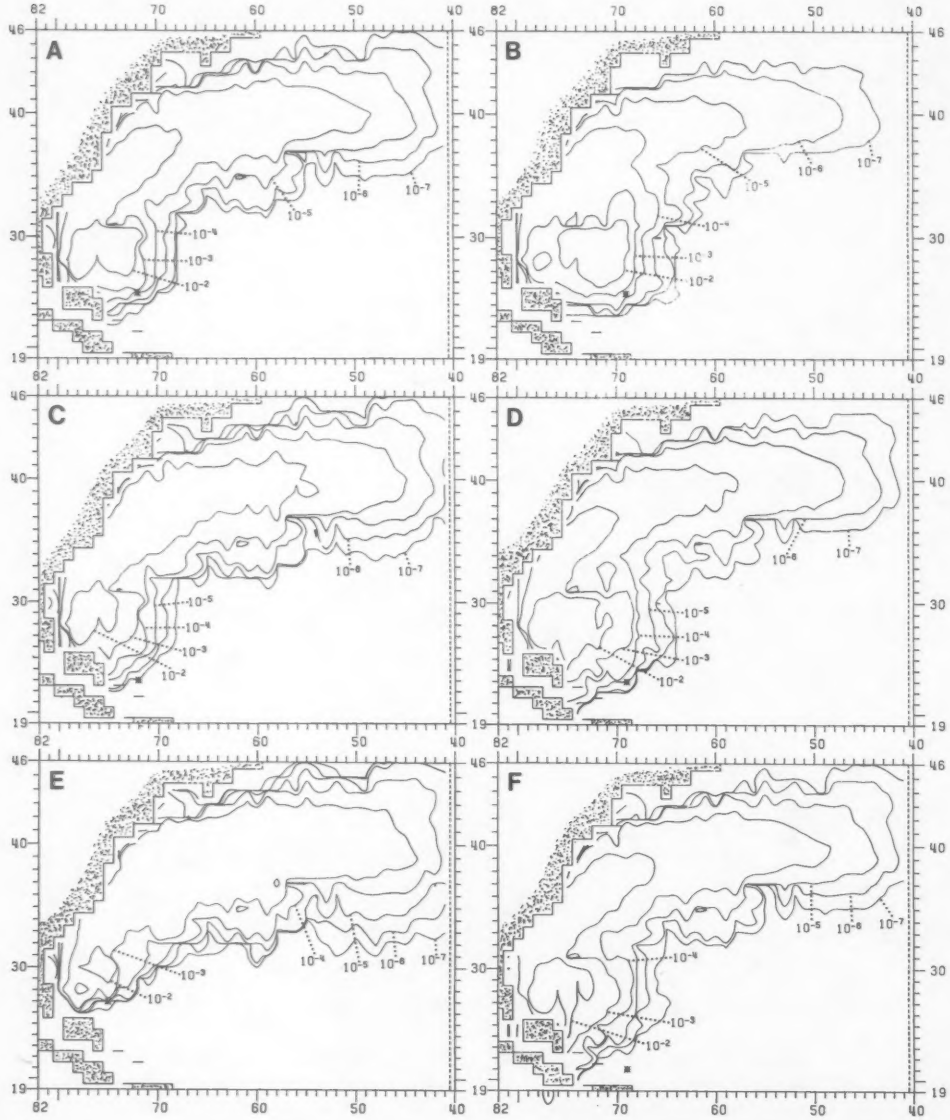

FIGURE 6.—Concentration contours of American eel leptocephali after 150 d of drift (29 July).

Distribution of Leptocephali After 210 Days of Drift

The patches of higher concentration persisted offshore of Florida and the Gulf Stream in all runs during the remainder of the summer (except E) and up to 7 mo after drift began, although they were beginning to dissipate (Fig. 7; 27 September). The cluster analyses still discriminated unequivocally between the patches and the lower concentrations to

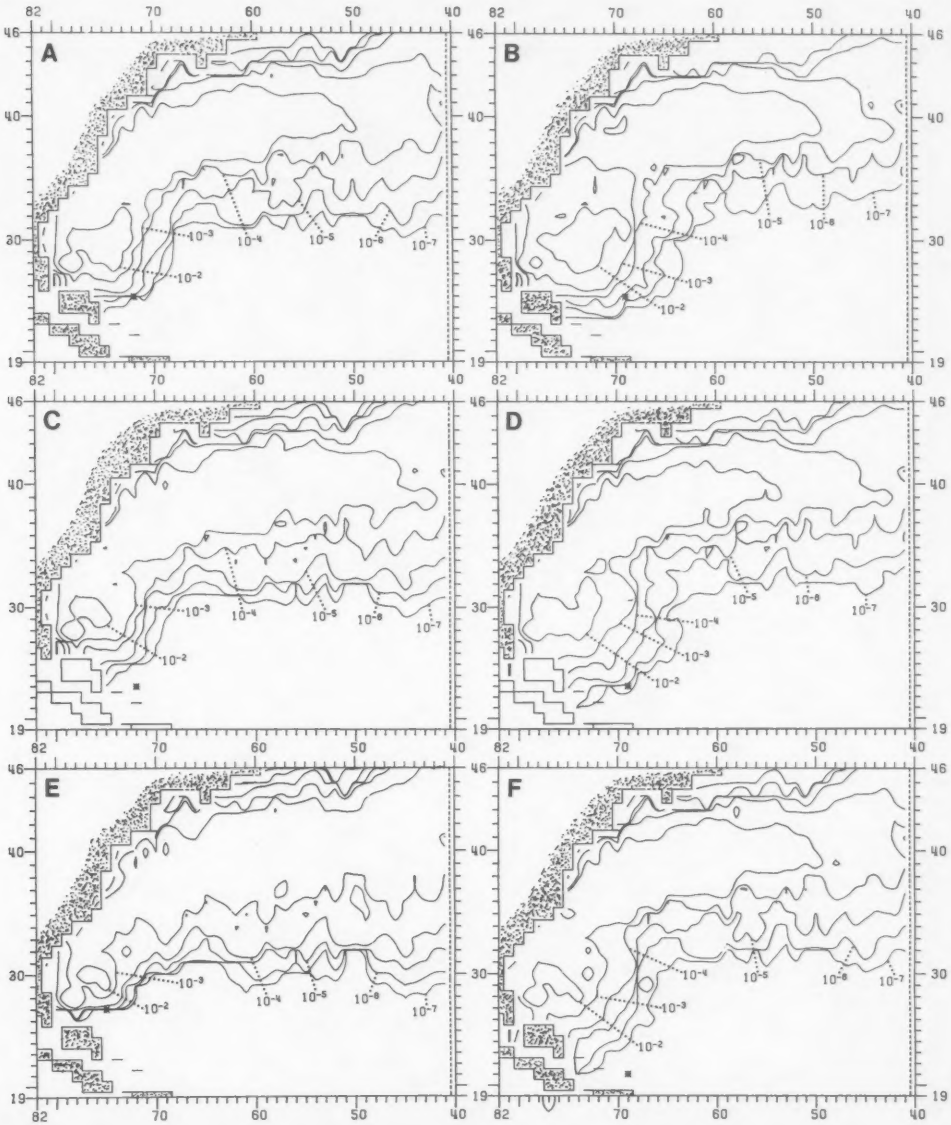

FIGURE 7.—Concentration contours of American eel leptocephali after 210 d of drift (27 September).

the immediate north in runs A and B and, to a lesser extent, in runs C, D, and F.

North of the patches the broad areas of uniform concentration were maintained and expanded by the continued entry of leptocephali into the Gulf Stream. This region extended along the North American coast to lat. 38°N, at which point it curved out into the Atlantic. It was best represented by the 10^{-3} contours in runs A, C, D, and F. The pattern was similar for run B, but the radial expansion of the main patch

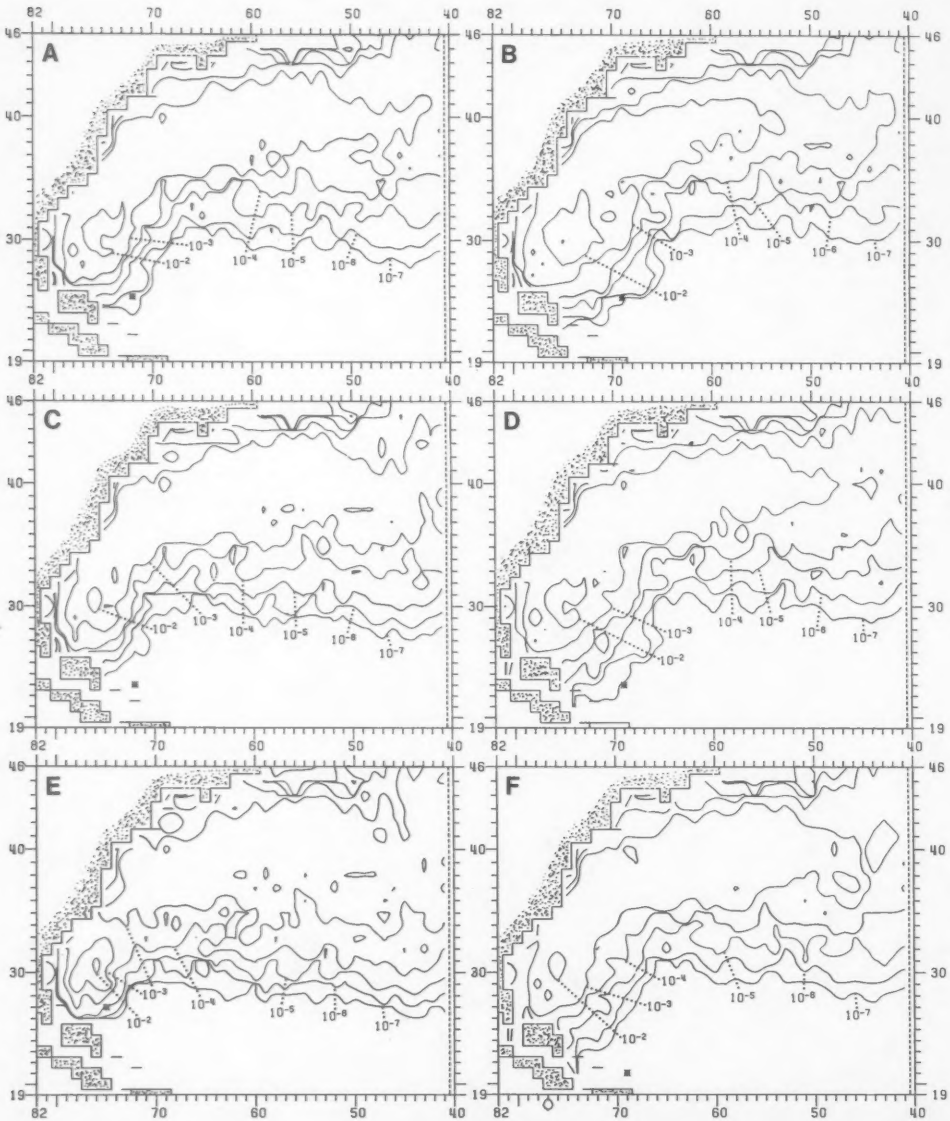

FIGURE 8.—Concentration contours of American eel leptocephali after 270 d of drift (26 November).

had continued. In most runs the plumes of leptocephali in the Gulf Stream had widened, so that concentrations $>10^{-7}$ were present across the modeled area between lat. 31° and 46°N. In run E the 10^{-3} concentrations extended completely from the patch area offshore of Florida to the right border of the modeled area.

Distribution of Leptocephali After 270 Days of Drift

Nine months after starting the leptocephali in runs A, C, D, and F had been distributed completely along the course of the Gulf Stream (Fig. 8; 26 November). There were very large areas with concentrations between 10^{-3} and 10^{-2} that spanned the modeled area from offshore of Florida to near the eastern border at long. 40°W. Run B still appeared to be in the process of developing the same distributional pattern as the others, because its pattern resembled those of the others 2 mo earlier. Leptocephali had progressed farthest in run E, in which the 10^{-3} concentrations were moving away from the mid-Atlantic coast.

At day 270 the simulations were halted, as some leptocephali would have begun metamorphosis to the glass eel phase by late November (Kleckner and McCleave 1980). It is unknown what behavioral components a glass eel or large leptocephalus may contribute during oceanic transport.

European Eel Drift Simulation

A simulation of European eel leptocephalus drift was done with the starting point at lat. 27°N and long. 57°W, and the starting date as 15 April. After 45 d of drift the larvae had spread to the northwest (Fig. 9A;

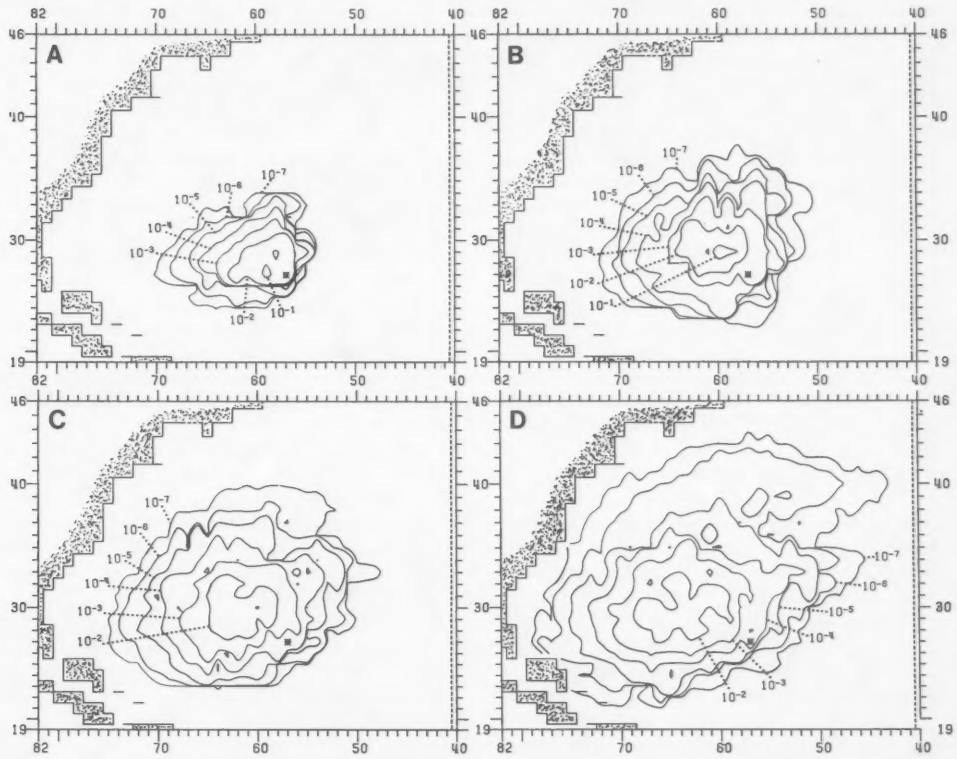

FIGURE 9.—Concentration contours of European eel leptocephali, expressed as a proportion of the starting concentration. Leptocephali were begun at the point marked with an × in Figure 1. A: contours for 30 May, 45 d after the 15 April start. B: contours for 29 July, 105 d after starting. C: contours for 27 September, 165 d after starting. D: contours for 26 November, 215 d after starting.

30 May). Two months later the 10^{-2} enclosed about the same area as before, but it had moved a few degrees to the northwest of the starting location (Fig. 9B; 29 July). The lower concentrations continued to spread, and dispersal occurred in most compass directions. By day 165, the lower concentrations had expanded still further, although concentrations $>10^{-2}$ maintained approximately the same position (Fig. 9C; 27 September). This same pattern of dispersal continued to day 215 of drift, at which point the concentrations $<10^{-5}$ at the northern limits of the distribution showed signs of being captured by the Gulf Stream (Fig. 9D; 26 November). The simulation was halted at day 215.

DISCUSSION

The simulations revealed several previously unsuspected features of the leptocephalus drift migration, such as the patch formation offshore of Florida and the Gulf Stream. This is in spite of the simplifications and assumptions that were made in a model encompassing such a large geographic area. The boundaries, currents, and eddy diffusivities all provided only an approximation to the physical system. Nonetheless, interpreting the simulation output using the available information on leptocephalus distribution and the eel's life history indicates that the model has realistically reproduced the large-scale features of the drift migration.

The simulated drift of American eel leptocephali can be divided into four phases, the first being initial northwest transport following spawning. This transport was largely on the Antilles Current, which flows northwesterly on a course parallel to the northeastern border of the Bahama Islands chain (Fig. 2). The extent of the initial larval transport depended on the starting location's position with respect to this current. Larvae started farther northeast in the Sargasso Sea (point B and other simulations not shown here) showed less unidirectional movement than those started in or nearer the Antilles Current. This current clearly appeared in ships' drift data for May (Fig. 2) and other late winter and spring months, so its effects in the simulations were no surprise. However, there are questions concerning the existence of the Antilles Current (Ingham 1975; Gunn and Watts 1982). Gunn and Watts (1982) showed that the Antilles Current was present in January-February 1973, but that the region was dominated by eddies in July-August 1972. They speculated that the Antilles Current may only exist seasonally. Its presence in January-February 1973 must have dominated the drift of newly hatched leptocephali from early spawning in that year. If the Antilles Current is seasonal, the question important to eel biology is how long does it persist through the spring and summer? The Antilles Current was important in the simulations from the time of spawning up to May-June. After that its influence on the distribution of 0-group leptocephali diminished, and by July-August, when Gunn and Watts (1982) did not find the current, most of the larvae were north of lat. 25°N. A study like that of Gunn and Watts is clearly needed for the months between February and July, and particularly for April and May.

There was little eastward transport from the starting locations in all American eel simulations, including those in which larvae were started along long. 66°W (not pictured in this paper). Schoth and Tesch (1981) collected American eel leptocephali east of long. 69°W (the longitude of the easternmost starting points in the simulations presented here), although the numbers of larvae they caught declined rapidly east of long. 65°W. Transport to the south was also minimal in the simulations, and few leptocephali entered the Caribbean. The simulations do not adequately explain the presence of leptocephali that have been collected in the Caribbean and Gulf of Mexico, and in particular the presence of young leptocephali near the Yucatan peninsula (Kleckner and McCleave 1980) was not reproduced. American eel spawning in the Caribbean remains a viable explanation for these collections.

The simulated drift of leptocephali south and west of the Bahamas must be interpreted cautiously, because this region's complicated bathymetry and currents were not well represented in the model. However, there were some striking correspondences between the simulations and the actual collection data for this region. Smith (1968) reported 10 May as the earliest collection date for 0-group leptocephali in the Straits of Florida between the Bahamas and Florida; Figure 3F shows larval concentrations of 10^{-6} (proportion of the starting concentration) had arrived in the Straits of Florida around 30 March, and by 30 April the concentration had increased to 10^{-4} (Fig. 4F). Kleckner and McCleave (1980) reported the collection of 0-group leptocephali in the Bahama Island chain in April to June, and the first collections of larvae in the Straits of Florida in May. Smith (1968) gave 28 August as the latest collection date of 0-group larvae in the Straits of Florida, and by that date most of the leptocephali in the simulations had departed the area as well.

The formation and maintenance of a patch of leptocephali north of the Bahamas and east of Florida and the Florida Current-Gulf Stream system were the

second phase in the simulated drift migrations. Regardless of starting location, most larvae converged upon the area and became part of this patch, except those that entered the Florida Current by the route south of the Bahamas. Gunn and Watts (1982) found evidence in the January-February 1973 data of a large anticyclonic eddy in the region of this patch formation (cf their figure 3D). If this eddy is a permanent or seasonal feature, it has substantial implications for American eel leptocephalus drift. It could be reasonably assumed that leptocephali collect in the eddy each year and that this patch phase is an integral part in the transport of most American eel leptocephali.

Transport of larvae from the patch and into the Gulf Stream seems to have been a result of turbulent diffusion, rather than advection, since currents east of the Florida Current are weak (Fig. 2). In the model, entry into the Gulf Stream was an example of large-scale shear induced diffusion, where large differences in adjoining northward current velocities resulted in concentration gradients down which a diffusive flux occurred. Whether this is the phenomenon that facilitates actual entrainment of leptocephali into the Gulf Stream is problematic. Alternatively, Gulf Stream cold-core rings occur in this area (The Ring Group 1981), and it may be that Gulf Stream eddies and meanders act to capture larvae.

The leptocephalus collection data are still inadequate to confirm the presence of a leptocephalus patch offshore of Florida and the Gulf Stream. However, there is empirical evidence that this is indeed the region where most leptocephali enter the Gulf Stream system. Kleckner and McCleave (1982) studied near synoptic collections of leptocephali taken on four transects of the Florida Current and Gulf Stream between 26 July and 16 August 1978. There were substantially higher concentrations of leptocephali in the waters sampled on the northern transects than there were in the southern ones (Fig. 10), indicating a significant input of leptocephali from the western Sargasso Sea. Combined with the present work, the studies of Kleckner and McCleave (1982) and Gunn and Watts (1982) indicate that processes important to the leptocephalus drift migration occur east of Florida and that further research should concentrate on this region.

The prolonged existence of the leptocephalus patch offshore of Florida and the Gulf Stream and the continuous capture of larvae by the Gulf Stream resulted in the broad and surprisingly uniform distribution of leptocephali along the North American coast. This transport along the North American coast formed the third phase of the drift migration. The patch can be viewed as a mechanism causing a more uniform distribution of leptocephali than would otherwise occur. Before developing the simulation model it had been

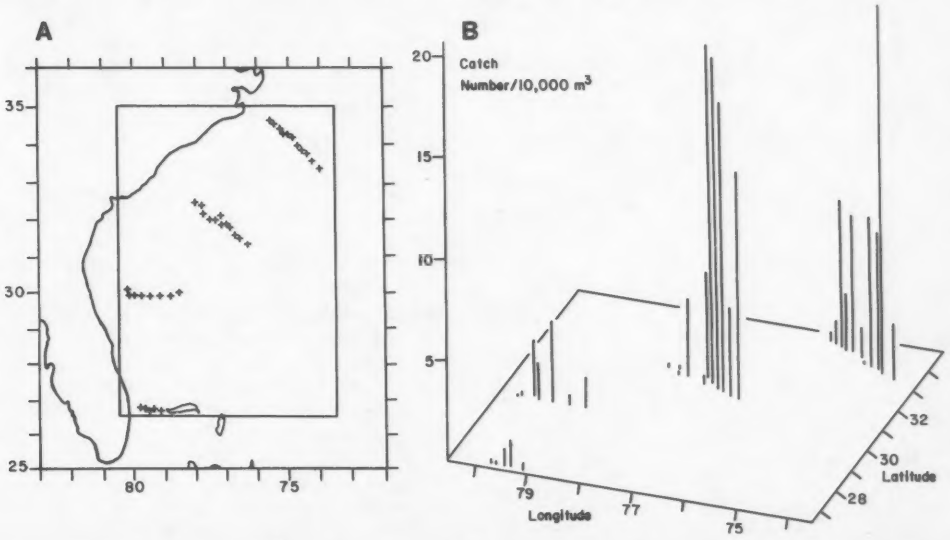

FIGURE 10.—A: Station positions on transects where American eel leptocephali were taken in the Gulf Stream system. B: Catches of leptocephali on the transects. Data from Kleckner and McCleave (1982).

assumed that leptocephali were quickly captured by the Gulf Stream and carried north and east, and it had been unclear how significant numbers of larvae remained in the southern portion of the eel's range. It is remarkable that a majority of the larvae remained so far south for such a prolonged period of time in the simulations.

Leptocephalus collections have not been made as systematically north of lat. 30°N as they have to the south, so it is difficult to compare the simulation results with the collection data north of this latitude. Kleckner and McCleave (1980, 1982[6]) stated that American eel leptocephali are abundant in the Gulf Stream from July through September, and the distributions of leptocephali they presented for these months correspond well with the simulation distributions (Fig. 11).

Up to about lat. 38°N the simulated concentrations formed wide bands along the coast; however, the simulations did not indicate how leptocephali in the eastern edges of the bands would move west towards the coast. The possibility of a behaviorally based, directed movement cannot be dismissed as unnecessary. Alternatively, it could be that these larvae are transported to Europe, or simply perish. McCleave and Kleckner (1982) demonstrated that in the tidal portion of an estuary American glass eels achieved upstream transport by selectively rising into the water column during flood tides. This has also been demonstrated for European eels (Creutzberg 1961), and it is certainly possible that larval and juvenile eels could utilize this mechanism in offshore tidal areas such as Georges Bank (Magnell et al. 1980).

There are abundant examples in the literature of stochastic events whereby leptocephali could also be transported inshore. Recent examples include Gulf Stream intrusions off St. Augustine, Fla. (Atkinson et al. 1978) and in Onslow Bay (Blanton 1971), Gulf Stream frontal eddies off Jacksonville, Fla. (Yoder et al. 1981), and Gulf Stream intrusions along the New York Bight (Judkins et al. 1980). Cox and Wiebe (1979) discussed the mechanisms by which oceanic plankton are transported into the Mid-Atlantic Bight, such as Gulf Stream warm-core rings and meanders. These meso- and finer scale features all surely transport leptocephali, but they were not directly incorporated into the model, except as their effects were represented with other turbulent motions by the eddy diffusivity terms. It seems maladaptive for leptocephali to rely upon such unpredictable features to facilitate a migration that occurs with annual regularity.

Eastward transport into the North Atlantic on the Gulf Stream was the fourth and final phase evident in the simulations. These last simulation phases may not have accurately represented the eel's migration, because leptocephali begin metamorphosis to the glass eel stage as early as October (Kleckner and McCleave 1980), and it becomes questionable as to whether the eels were still drifting passively. Unless the loss of eels due to transport out into the Atlantic is substantial, it seems that by this point the eels must modify their drift in some way if they are to avoid transport to Europe. A small number of American eel are in fact found in European waters (Boëtius 1980). In the passive drift simulations, only a small portion of the larvae entered the Gulf of Maine, although this region also has complicated currents not accurately represented in the model. Meanders of the Gulf Stream will carry some larvae near the northeastern North American coast, as it has for other species (Colton et al. 1962; Markle et al. 1980). The transport of leptocephali out into the Atlantic was centered on lat. 40°N, and this agrees well with the results of Richardson (1981), who tracked buoys drifting on the Gulf Stream.

The European eel spawns in a region of weak and indeterminate currents, and in the simulation this resulted in a slow spreading of the leptocephali throughout the Sargasso Sea. It is clear that if the simulation presented in Figure 9 were continued, the

[6]Kleckner, R. C., and J. D. McCleave. 1982. Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current system. Unpubl. manuscr., 46 p. Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469.

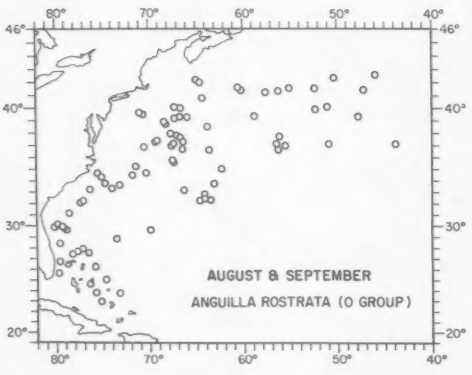

FIGURE 11.—Locations in the North Atlantic Ocean where one or more *Anguilla* leptocephali have been collected during August and September. Compare with Figures 6 and 7. From Kleckner and McCleave (text footnote 6).

leptocephali would simply have continued to spread, with those moving west and north gradually entering the Gulf Stream. This simulation result agreed with the "moderate to rich" catches of 1-group European eel leptocephali reported by Tesch et al. (1979) as being present north of lat. 26°N and between Bermuda and Europe. Such gradual dispersal also makes it not surprising that the European eel spends 3 yr as a leptocephalus before reaching Europe.

In summary, the simulations have reproduced the important features of the leptocephalus drift migration. Some of the features, such as the patch formation offshore of Florida, were previously unsuspected, but seem highly plausible when considered in combination with the hydrographic data and the leptocephalus collection data for that region. This patch, and the remainder of the predicted leptocephalus distribution, remains to be verified by intensive and systematic sampling.

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WALRUS, *ODOBENUS ROSMARUS*, FEEDING IN THE BERING SEA: A BENTHIC PERSPECTIVE

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AND LLOYD F. LOWRY[2]

ABSTRACT

Walrus, *Odobenus rosmarus*, feed primarily on benthic bivalves and create a distinct record of their feeding activities on the sea floor. The record consists of furrows, pits, and discarded bivalve shells which were observed and sampled with scuba. Documentation of this benthic feeding record suggested that walrus commonly search for visually conspicuous prey by sight; that, in addition to "rooting" with the snout and vibrissae, walrus excavate bivalve prey by hydraulic jetting; that tusks are not used to excavate prey; and that all prey are excavated before consumption, which generally occurs close to the site of excavation. The mechanism of consumption appears to involve suction from between the shells. Continuous pit-furrow systems indicate the number of prey consumed in single dives, and suggest that a walrus can locate, excavate, and consume more then six clams per minute. The abundance of small infauna that are not walrus prey (e.g., polychaete worms, small bivalves, and crustaceans) was lower inside all excavations, indicating that the structure of bottom communities is highly modified by the extraction of a few large prey.

Marine mammals are observed primarily at the sea surface. Yet many important activities, especially feeding, occur underwater beyond the view of surface observers. While informative glimpses of feeding activities are sometimes obtained at the water surface (e.g., Watkins and Schevill 1976, 1979; Würsig and Würsig 1980), and the types of foods consumed are indicated by contents of gastrointestinal tracts (e.g., Lowry et al. 1980; Lowry and Frost 1981), knowledge of foraging behavior and the community role of marine mammals is generally poor. Electronic tags, depth recorders, and other instrumentation are improving this limited view (e.g., Watkins et al. 1981; Kooyman 1981). However, the greatest opportunities for studying the feeding ecology of marine mammals may involve species that prey on benthic organisms.

Bottom-feeding marine mammals often feed in shallow water, where general feeding grounds usually are known and local feeding areas can be relocated. Because benthic habitats and bottom prey are relatively immobile, prey communities can be sampled with considerable accuracy and precision, and can be experimentally manipulated as well. Largely for these reasons, we understand more about the community role of the sea otter, *Enhydra lutris*, a bottom feeder, than any other marine mammal (Estes and Palmisano 1974; Dayton 1975; Estes et al. 1978, 1982; Simenstad et al. 1978; Duggins 1980). In contrast to the very few species of bottom feeders, most marine mammals feed on mobile prey in the water column where foraging activities are difficult to observe, and no record is made. Nektonic prey are extremely difficult to sample quantitatively. Even if a feeding event were observed, the dynamic nature of prey patches and the pelagic habitat preclude direct measurement of the effect of mammal predation on prey communities.

Some bottom-feeding marine mammals leave a record of their feeding activities in soft-sediment environments. The record primarily consists of pits and furrows made in the sea floor. For example, the gray whale, *Eschrichtius robustus*, produces large, bowl-shaped pits while feeding on benthic infauna, especially amphipod crustaceans (Oliver et al. 1983). Gray whales capture and consume invertebrate prey by suction, but also kill, injure, and displace nonprey, modify local habitats, and attract scavenging animals to these excavated bottoms. Walrus; bearded seals, *Erignathus barbatus*; sea otters; dugongs, *Dugong dugon*; and manatees, *Trichechus* spp., also feed in soft-sediment habitats, but only the walrus and gray whale depend primarily on infaunal prey (Anonymous 1978).

Walrus are a common and conspicuous element of the marine mammal fauna inhabiting arctic and subarctic waters of the Northern Hemisphere. They are particularly abundant in the Bering and Chukchi Seas, where they forage among the bivalve communities found on the broad Beringian platform. The contents of numerous gastrointestinal tracts indicate

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[2]Alaska Department of Fish and Game, Fairbanks, AK 99701.

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that bivalve mollusks are the primary prey (Fay 1982). However, because gastrointestinal samples are extremely difficult to relate to a particular feeding habitat and walrus feeding has not been observed in the field, present knowledge of foraging behavior largely depends on morphological arguments and observations of captive animals (Fay 1982). We cannot evaluate walrus disturbance of bottom communities from gastrointestinal samples. The diet and feeding method of walrus provide an opportunity to explore their feeding ecology by examining records of foraging activity on the sea bottom.

There are three principal objectives of this paper: 1) To describe the benthic feeding record of the walrus; 2) to demonstrate that the record provides important insights into patterns of searching, capturing, and consuming prey; and 3) to suggest the roles walrus play in structuring soft-bottom communities.

STUDY AREA

All of our observations and sampling were done near Nome, Alaska, in the northern Bering Sea (Fig. 1). The bottom is gently sloping, with extensive flat regions of fine and muddy sand (Sharma 1974). Bottom waters are cold (1°-8°C), and temperatures fluctuate seasonally (Muench et al. 1981). Water clarity is poor, usually allowing 0.5 to 1.5 m of visibility, but is occasionally 2 to 8 m. Sea ice forms during the fall and persists until late spring or early summer. Fast ice is relatively persistent nearshore, but offshore ice patterns are highly variable, particularly the occurrence and movement of the pack ice (McNutt 1981; Stringer 1981; Ray and Dupré 1981). No ice gouging of bottom sediments or gas cratering occurs in the study area (Larsen et al. 1979). Walrus are strongly associated with sea ice, where they haul out to care for young and to rest, often between foraging activities (Fay 1982). Large numbers of walrus pass through the study area, particularly during the spring northward migration (May-June). Small numbers may be present there during other months as well (Fay 1982; pers. obs.). Bearded seals are also abun-

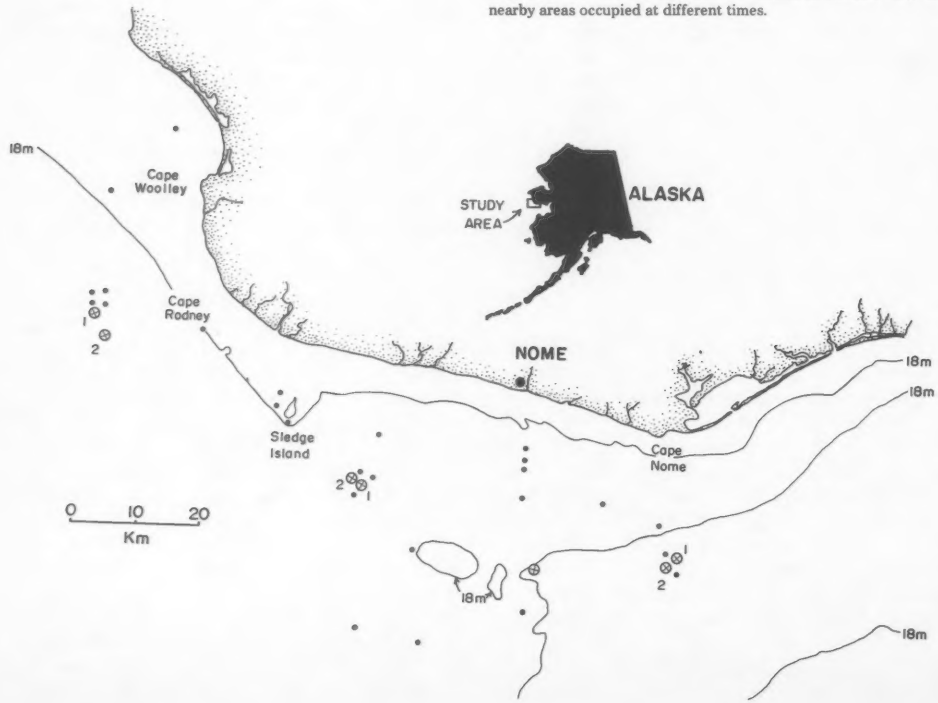

FIGURE 1.—The major diving stations (large open circles with × in center) and other sites (small closed circles) surveyed by divers in May-June 1981 near Nome, Alaska. Numbered stations refer to nearby areas occupied at different times.

dant in the area during the spring (Lowry et al. 1980), but gray whales are seen infrequently (pers. obs.). The biomass of benthic animals is dominated by bivalve molluscs and echinoderms with large numbers of a few sedentary polychaete worms (Stoker 1978). The number and biomass of crustaceans are much lower in the study area compared with the central and western parts of the northern Bering Sea (Stoker 1978).

Field work was done from 22 May to 7 June 1981. Remnants of shore-fast ice moved away from Nome several days before our arrival. Well-developed pack-ice and large groups of walrus were observed in the general study area during the preceding month. These animals probably fed in the region for at least a month before our arrival. Therefore, the benthic feeding record was likely to be quite recent. No walrus were seen in the study area after the sea ice moved offshore around 15 May 1981.

METHODS

Thirty-three dives were made south and west of Nome (Fig. 1). At each site, divers using scuba thoroughly searched the bottom for traces of walrus feeding activity. The benthic feeding record was quantified at only several sites where feeding traces were found. Here, discarded bivalve shells were collected, and the distance to the nearest pits and furrows was recorded. Pit and furrow dimensions were measured, as well as the number of pits in a patch, and the area of bottom containing each distinct patch of pits. A patch of pits was considered distinct when no additional pits were found within 5 m of the group. Water clarity of <1 m limited the patch size observations in all areas except Cape Nome. Shell lengths and breaking strengths (using a hinged plate that was calibrated to pounds of pressure) were measured at the laboratory.

Small benthic infauna that are not walrus prey were sampled directly in feeding excavations, and in adjacent undisturbed bottoms with hand-held corers (area $= 0.0075$ m^2; depth $= 12$-15 cm). Samples were washed over a 0.5 mm screen, and preserved in a solution of 4% formaldehyde. Animals were identified to the lowest possible taxon and counted. Although juvenile bivalves and small species were adequately sampled by the corers, larger individuals were not, particularly the major walrus prey, *Macoma* spp., *Mya truncata*, and *Serripes groenlandicus*. However, the siphons and siphon burrows of the deep-burrowing clam, *M. truncata*, were counted in 1 m^2 areas to estimate the abundance of these large individuals. Sediment consolidation was measured with a simple penetrometer, which was a weighted rod (0.5 kg) dropped through a cylinder resting on the bottom. Penetration was estimated as distance of rod penetration into the surface sediments (e.g., Ronan 1975).

RESULTS

Benthic Feeding Record

We observed two basic types of excavations, furrows and pits. In both cases, shells of the excavated clams were discarded close to excavations. Therefore, different pits and furrows were easily linked to the species of excavated bivalve prey. There were three principal bivalve prey, *Mya truncata*, *Serripes groenlandicus*, *and Macoma* spp. (mostly *M. calcarea*). These groups are recognized as major prey by Vibe (1950) and Fay (1982). Feeding records generally contained one or two types of excavations: Furrows, *Mya* pits, or a mixture of *Mya* and *Serripes* pits. The relative abundance of discarded shells corresponded to the primary type of excavation in each area. For example, 92 to 100% of the shells were *Mya truncata* at stations that primarily had *Mya* pits; 76 to 83% of the shells were *Macoma* spp. at stations that primarily had *Macoma* furrows; and *Mya truncata* and *S. groenlandicus* shells were both abundant at stations that had mixed pits (Table 1). Bivalve prey thus were identified by discarded shells and by ex-

TABLE 1.—Excavation type and percentages of discarded shells from the three major prey found at the main feeding sites near Nome, Alaska. Percentages are based on the number of reconstructed whole clams.

Location	Depth (m)	Primary[1] excavation type	Percent of discarded shells			No. of bivalves
			Mya truncata	*Serripes groenlandicus*	*Macoma* spp.[2]	
Cape Rodney-1	24	*Mya* pit	100	0	0	17
Cape Rodney-2	24	furrow	18	6	76	17
Sledge Island	24	furrow	10	10	83	41
Nome	24	mixed pit	41	54	5	35
Cape Nome-1	17	*Mya* pit	92	4	4	26
Cape Nome-2	17	mixed pit	21	79	0	164

[1]Areas contained either mostly *Mya* pits, mixed pits of *Mya* and *Serripes*, or mostly furrows with *Macoma*.
[2]Primarily *Macoma calcarea*.

cavation morphology. Each excavation was linked to a particular species of clam, and a larger region (dive station) was characterized both by the primary type of excavation and by the most abundant shells. Because each of two divers traveled at least 50 m and often over 100 m per dive, the primary type of excavation was easily assessed, albeit qualitatively, despite the poor water clarity. Benthic feeding records were located on 18 of 33 dive sites, but were only well quantified at 6 of the 18 sites (Table 1).

Furrows

The most extensive and distinct furrows were found near Sledge Island (Table 1). Water clarity in this area was relatively poor (about 1 m), but was adequate to see furrow widths and to trace lengths. By swimming rapidly over a long distance (>50 m), we estimated qualitatively that at least 40% of the bottom was furrowed at one Sledge Island dive site. Furrows generally formed a complex maze of excavations, but discarded shells always were abundant (as many as 5-10/10 m^2) within and along the furrow edges and were rare (<1/10 m^2) on undisturbed bottoms between furrows. The average furrow width was 45 cm and depth was 17 cm (Table 2). *Macoma* spp. were primarily excavated from furrowed bottoms (Table 1).

TABLE 2.—Morphological differences between the three major types of excavations of the walrus. Means and 95% confidence limits (sample size).

	Diameter or width (cm)	Depth (cm)
Mya truncata pit	30±1 (30)	32±3 (10)
Serripes groenlandicus pit	14±2 (9)	11±3 (14)
Macoma spp. furrow	45±3 (7)	17±2 (7)

Pits

Three distinct types of pits were made in excavating *Mya truncata*, *Macoma* spp., and *Serripes groenlandicus*. The pits differed in diameter or depth (Fig. 2, Table 2), reflecting a species position in the sediment.

Mya pits had a deep central shaft (Fig. 2). Divers readily identified these pits by thrusting a fist into a shaft. *Mya truncata* has a long, tough siphon and lives deep in the sediment (about 30 cm). Eighty-nine percent ($n = 190$) of the *Mya* pits contained only a *Mya* shell within 1 m of the pit.

Macoma pits were similar in diameter to *Mya* pits, but lacked the central shaft. They were relatively rare, as furrows were the primary excavations associated with *Macoma* shells (Table 1). *Macoma* spp. generally lives <20 cm into the sediment, and has a shorter siphon than *Mya truncata*.

The largest *Serripes* pits were much smaller than the *Mya* and *Macoma* pits (Fig. 2). Small *Serripes* pits were impossible to distinguish from sea star pits and surface irregularities. Some large *Serripes*-type pits may be made by larger sea stars (*Lethasterias* and *Asterias*). This bivalve has a short siphon, is a shallow burrower, and commonly occurs at the sediment surface. *Serripes* shells were conspicuous on the sediment surface. Therefore, although either the shells or pits of *Mya truncata* and *Macoma* spp. could be counted to estimate prey consumption, only the shells provided an adequate estimate of the number of *S. groenlandicus* eaten by walrus.

Pit-Furrows

Pit-furrow systems consisted of a series of pits connected by a shallow, continuous, and distinct furrow (Fig. 3). These systems were less common than the isolated pits or deeper furrows, and were found only at Cape Nome. Species excavated in the pit-furrow systems were primarily *Mya truncata* and *S. groenlandicus*.

Shells

The shells of primarily three groups of bivalves, *Mya truncata*, *Serripes groenlandicus*, and *Macoma* spp., were observed on the sea floor (Fig. 4). *Macoma* and *Serripes* shells were commonly attached at the umbus. About 6 to 8% of the shells from these groups were broken, while 78% of the *Mya* shells were broken (Table 3). Greater breakage of *Mya* shells appeared to be related to shell hardness (Table 3), and not necessarily to a different feeding method. The outer lining of the siphon (the periostracum) was attached to 83% of the *Mya* shells ($n = 65$), and the distal end of the siphon commonly was intact.

TABLE 3.—Percentage of broken shells found in major prey species (based on number of reconstructed whole shells), and an index of shell hardness.

	No. of bivalves	Percent broken	Shell hardness[1]
Mya truncata	96	78	4.9±1.7
Macoma spp.	32	6	7.2±2.3
Serripes groenlandicus	154	8	7.2±1.2

[1] Pounds of pressure required to break a single valve. Means and 95% confidence limits in 10 trials.

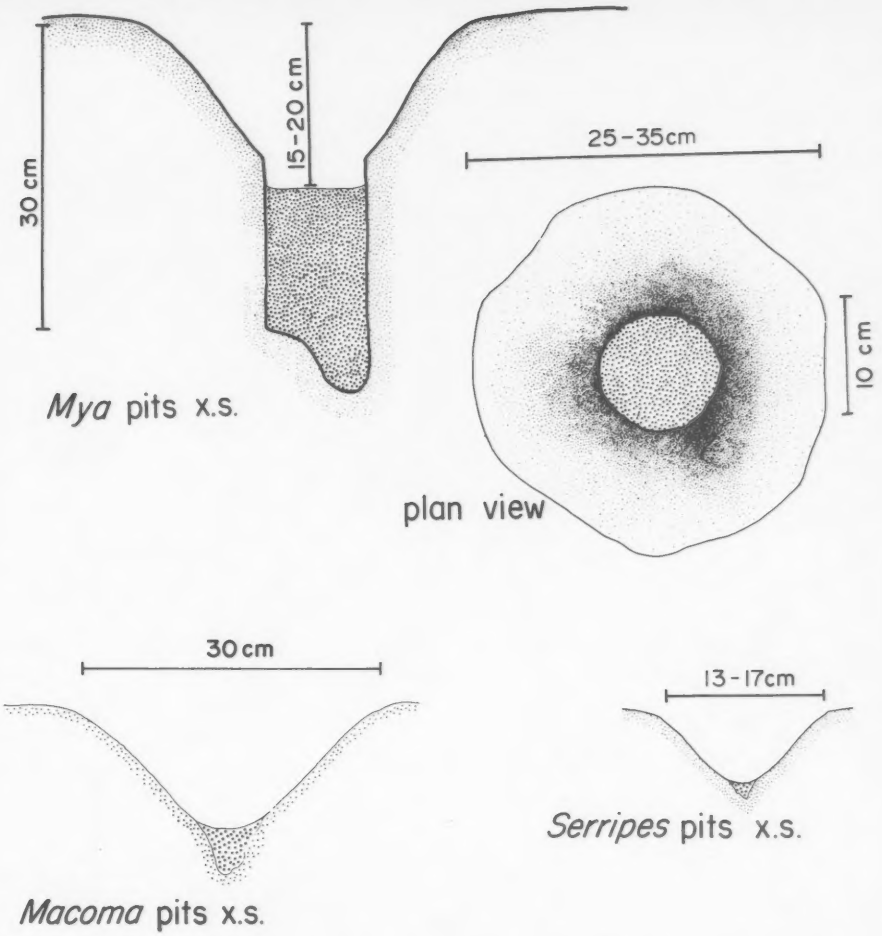

FIGURE 2.—Illustrations of the large *Mya truncata* and *Macoma* spp. pits, and the smaller pits created by excavating *Serripes groenlandicus*.

Evidence for Single Diving Events

Mya pits generally were found in distinct groups with a distance of at least 5 m between patches of pits. There was no significant difference between the number of pits per patch or the area covered by a group of pits when two similar dive sites were compared from Cape Nome (Table 4). Patches included from 1 to 20 pits, which may represent the activities of a walrus during a single dive.

We found one excellent record of the number of clams taken in a single feeding event in a pit-furrow system located off Cape Nome (Fig. 3). The pits or shells of 19 *M. truncata* and 15 *S. groenlandicus* were located in this continuous pit-furrow. Unfortunately, we could not survey the entire system because of a

TABLE 4.—Number of *Mya* pits found per group and area of the patches in two similar locations near Cape Nome. Means and 95% confidence limits in *N* samples.

	N	Cape Nome-2	*N*	Cape Nome-1	Prob.[1]
Pits per patch	15	6.1±2.6	12	5.6±3.2	$P>0.3$
Patch area (m^2)	15	10.6±7.6	12	18.0±9.8	$P>0.2$

[1] Probability of difference in *t*-test.

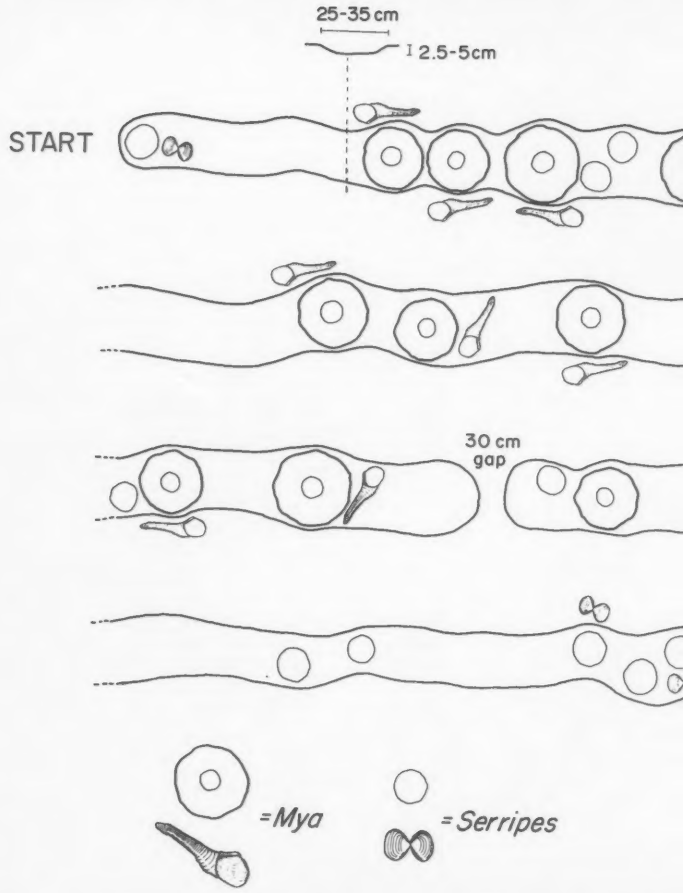

FIGURE 3.—A continuous pit-furrow system made by a feeding walrus showing pits foun

ts found with and without bivalve shells. Divers did not reach the end of the system.

FIGURE 4.—Shells of *Mya truncata* (A), *Macoma calcarea* (B), and *Serripes groenlandicus* (C) discarded by feeding walrus.

low air supply. Nevertheless, this incomplete record is the most accurate estimate of the number of clams it is possible for a walrus to excavate during a single dive.

Effects on Benthic Communities

Walrus undoubtedly have a significant effect on abundance and size distribution of bivalve prey. Because we did not obtain adequate samples of the large individuals in living bivalve populations, we could not compare availability of various sizes of prey with the sizes of prey consumed. Nevertheless, discarded shells indicated that walrus consumed relatively large individuals from the three principal groups of bivalves (Fig. 5).

It is important to determine whether walrus disrupt different nonprey populations while feeding in different local habitats. Core samples were taken to document the species composition and relative abundance of the smaller infauna, which could be displaced, injured, or killed during excavation of the large bivalve prey. These samples indicate that benthic infaunal communities were strikingly different at the major feeding sites near Nome (Table 5). The western areas were near Cape Rodney and were numerically dominated by tube-building polychaete worms, *Myriochele oculata*, and *Polydora flava flava*.

TABLE 5.—Abundant infauna found at the three major feeding sites of walrus. Mean numbers per 0.0075 m^2 with standard deviations in parentheses. P = polychaete; C = crustacean; O = ophiuroid; T = tunicate; Pr = protozoan.

	Cape Rodney-1 (24 m)	Sledge Island-2 (24 m)	Cape Nome-2 (17 m)
Myriochele oculata (P)	133 (55)	45.7 (10.6)	448 (116)
Polydora cf. *flava flava* (P)	302 (171)	0	0
Exogone sp. (P)	9.7 (3.5)	0	0
Sabellidae (P)	8.3 (5.1)	0	1.3 (1.0)
Syllis sp. (P)	7.7 (1.8)	0	0
Amphiodia craterodmeta (O)	1.7 (1.2)	205 (48)	5.7 (2.3)
Leucon nasica (C)	0	18.3 (0.4)	0
Oligochaeta	0	14.0 (11.0)	0
Rhizomogula sp. (T)	0	0	201 (71)
Protomedeia fasciata (C)	1.7 (1.2)	4.7 (2.7)	51.3 (47.5)
Gromia sp. (Pr)	4.7 (1.8)	0	34.2 (8.7)
Podocopids (C)	3.3 (2.0)	2.0 (1.0)	14.0 (4.2)

We located an excellent record of *Mya* pits and shells there (Table 1), and observed the siphons and siphon-burrows of large, living *M. truncata*. At Sledge

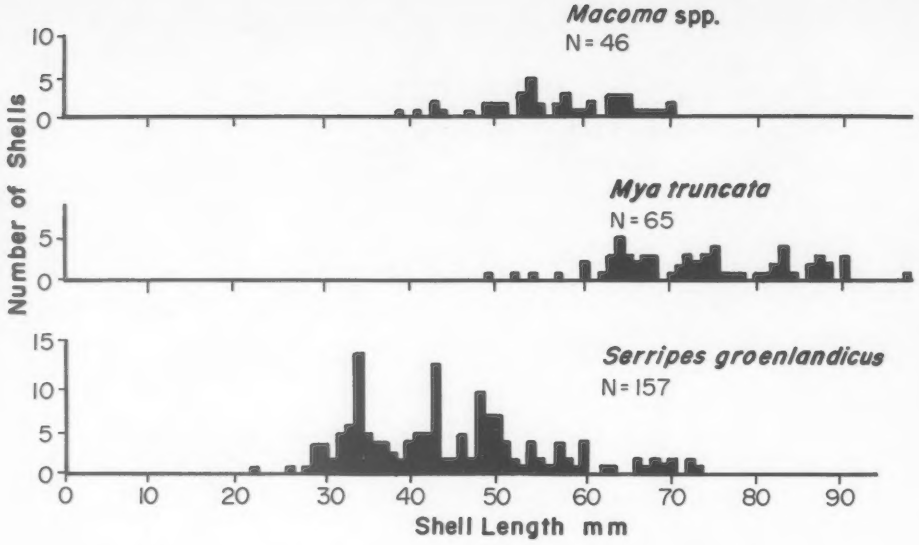

FIGURE 5.—Shell size of three groups of clams consumed around Nome, Alaska. Shells are from the benthic feeding record.

Island, the small ophiuroid, *Amphiodia craterodmeta* (disc diameter = 1-4 cm) was the most abundant species, and there was a record of furrowed sediment and *Macoma* shells (Table 1). Qualitative observations indicated few large, living bivalves, mostly *Macoma* spp. and fewer *Mya truncata*. Instead of a visually conspicuous tube mat of polychaetes, the bottom was covered with a dense carpet of interwoven ophiuroid arms. At Cape Nome, *Myriochele oculata*; the tube-building amphipod crustacean, *Protomedeia fasciata*; and the infaunal tunicate, *Rhizomogula* sp., were relatively abundant. *Mya truncata* was the major walrus prey taken at Cape Nome (Table 1) and was the only abundant large bivalve living here (>5/m²). The number of sea stars, primarily *Asterias amurensis*, increased from Cape Rodney to Cape Nome. They were the predominant large epifaunal animals.

The feeding activities of walrus produced similar changes in the structure of these different benthic communities. The feeding excavations we discovered probably were <1 mo old (see section on Study Area), and occurred in highly mixed gravel and sand, in sand, and in sandy mud. Sediments were significantly less consolidated ($t = 10.2$, $P<0.0001$) in *Mya* pits (penetration = 11.9 cm; $n = 15$) than in undisturbed sediments (penetration = 4.4 cm; $n = 15$). The biogenic structure of surface sediments in excavations was poorly developed compared with the adjacent bottom.

Despite differences in the structure of nonprey communities, most infauna were less abundant inside the recent walrus excavations from all feeding sites. With few exceptions, the abundances of major groups (Fig. 6) and numerically dominant species (Fig. 7) were lower inside pits (Cape Rodney, Nome, Cape Nome) and furrows (Sledge Island). One exception was the polychaete worm *Myriochele oculata* at one Sledge Island site (Figs. 6, 7). These individuals were not recently settled, but were large adults in well-developed tubes. Because this species was relatively immobile, tubes probably were concentrated passively in the furrow bottom during walrus feeding. The small (diameter <1 cm) infaunal tunicate *Rhizomogula* sp. was very abundant in the Cape Nome region, and apparently rolled into *Mya* pits during and after excavation. Its abundance was significantly higher ($t = 5.1$, $P<0.01$) in the bottoms of pits ($\bar{X} =$ 576 per core inside, 251 outside; $n = 6$). One or two larger epifaunal anemones also occurred in many excavations. We observed several of these individuals rolling across the sediment surface in strong currents. Scavenging lysianassid amphipods were abundant in only two cores from recent excavations at Cape Nome (61 and 43/core; 1/133 m²). These amphipods were rare in most core samples (<1/core;

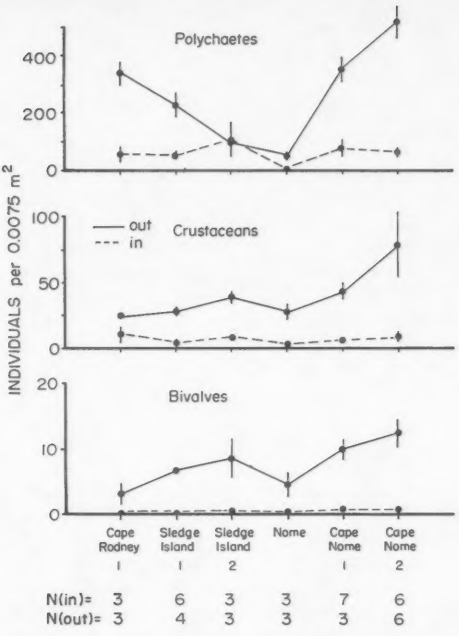

FIGURE 6.—Abundances of major infaunal groups inside and outside the furrows dug for *Macoma* spp. (Sledge Island), and the pits excavated for *Mya truncata* (all other areas). Means and standard errors in N cores.

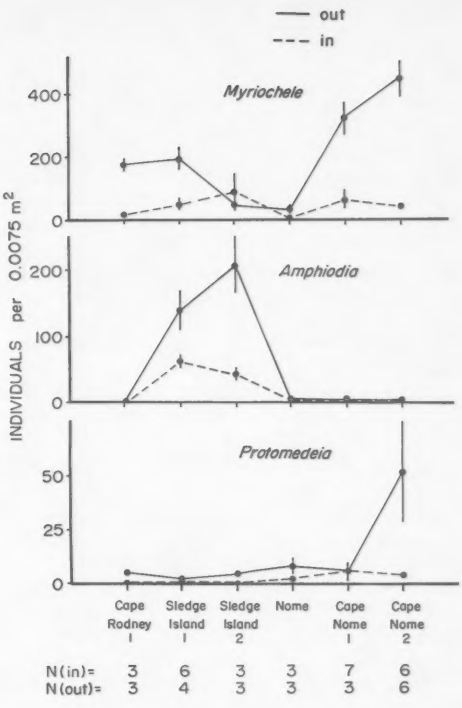

FIGURE 7.—Abundances of three numerically dominant infaunal species inside and outside walrus excavations. The polychaete worm *Myriochele oculata*, the ophiuroid *Amphiodia craterodmeta*, and the crustacean *Protomedeia fasciata*. See Figure 6 legend.

$n = 26$ cores). Lysianassids respond to various disturbances and are voracious scavengers (pers. obs.) that probably were attracted to the tissue on a discarded bivalve shell.

DISCUSSION

Walrus Feeding Behavior

Walrus are highly specialized for feeding on benthic infauna, especially bivalve molluscs (Fay 1982). Of other marine mammals, only the diet of bearded seals overlaps with the bivalve prey of walrus near Nome, but bearded seals have a much broader diet than do walrus (Lowry et al. 1980). Because bearded seals eat certain shallow-burrowing clams (e.g., *Serripes groenlandicus*) and rarely eat deep burrowers (e.g., *Mya truncata*), they cannot account for the diverse feeding records observed near Nome. No other biological or physical process can account for the record of excavations and discarded shells. While some large sea stars can make pits as large as the larger *Serripes* pits, none of the *Mya* and *Macoma* pits or the furrowed bottoms are produced by sea stars.

The low water clarity in the Bering and Chukchi Seas and the poorly developed eyes of walrus suggest that prey are not located by sight (Fay 1982). However, the benthic feeding records suggest that walrus often search for certain bivalves by sight. The most important evidence was the presence of many distinct, isolated pits with no indication of bottom disturbance between pits. These pits were made in excavating *Mya truncata*, the same species that divers routinely located by sight because of the large, conspicuous siphons. Apparently, walrus used the snout and vibrissae to search for prey without conspicuous siphons or shells (Fay 1982), as extensive furrowing only occurred in excavating *Macoma* spp., clams with small and cryptic siphons. These "rooting" activities clearly disturbed surface sediments and infaunal communities. Even the move-

ments of hermit crabs, gastropods, and sea stars produced distinct traces in surface sediments. Because the bottom was undisturbed around the isolated pits made in extracting the visually conspicuous prey, the snout and vibrissae were probably unimportant in locating these species.

The feeding excavations of walrus clearly indicate that clams are not excavated with the tusks. Fay (1982) gave a convincing argument based on anatomy and tusk abrasion patterns that the tusks are not used to excavate prey. Their main function apparently involves aggressive interactions, especially among the males (Miller 1975). None of the furrows or pits we discovered could be produced by plowing or digging with the tusks. As suggested by Vibe (1950) and Fay (1982), most excavations probably involve "rooting" with the snout and vibrissae. According to Fay[3], snout widths of subadult and adult walrus range from 29 to 41 cm for males and 23 to 35 cm for females. These sizes correspond exactly to the diameter of the upper portion of *Mya* pits and the width of furrows if the snout is swung in a narrow arc during excavation (Table 2).

We hypothesize that in addition to "rooting," a pulsing jet of water also was used to excavate prey. The walrus' mouth and tongue are well adapted for sucking and expelling water (Fay 1982) (a well-known fact to visitors who are sprayed regularly at Sea World Park in San Diego). Hydraulic jetting is the only feasible mechanism for producing the deep (30 cm) central shafts of *Mya* pits. These hydraulic pulses also may be used to produce furrows and other pits, probably in conjunction with snout and vibrissae movements. This idea was tested by constructing a suction-jet similar to the clam guns used to extract bait from intertidal mudflats. By manipulating the nozzle diameter and the volume of water exchanged per stroke, divers have produced excavations similar to the pits and furrows made by walrus.[4] A similar jetting process was observed in bat rays by Gregory et al. (1979), who suggested that it was used to excavate infaunal prey.

All clams were excavated prior to consumption. Shells were found on the surface of the sediment in a nonliving orientation. There was no evidence that biting (Vibe 1950) or suction was used to remove the soft parts of the clam while the shell was held in the sediment. Soft parts were clearly consumed near the sea floor, because discarded shells were closely associated with pits and furrows. The soft parts of clams probably were sucked from between the two shells (Vibe 1950; Fay 1982).

Perhaps the most exciting potential of the benthic feeding record is to quantify the activities of a single dive. The continuous pit-furrow system we discovered showed the location, excavation, and consumption of 34 clams along >60 m of the bottom. Over half of these clams (19) lived 30 cm deep in the sediment. At this water depth average dive times are about 5 min (Fay 1982), which suggests that one walrus ate more than six clams per minute. Divers can locate a number of long, continuous pit-furrow and furrow systems where the species, size, and number of prey can be measured. These may be the most accurate records of the diving and foraging activities of any marine mammal.

Effects of Bottom Disturbance

Walrus have an obvious impact on their large bivalve prey, but they also displace many of the small and abundant infauna that are not walrus prey. All the furrows and pits we observed were probably <1 or 2 mo, and probably <1 mo old (see section on Study Area). While there were dramatic differences between the structures of nonprey communities at the major feeding sites, the abundances of most small infauna were significantly lower inside all of the recent excavations (Figs. 6,7). The few exceptions were either immobile species that were passively concentrated in the excavations (e.g., *Myriochele oculata* and *Rhizomogula* sp.), or more motile species that may be attracted to the excavations or to scavenging events inside excavations (e.g., lysianassid amphipods). Walrus disturbance clearly produces new habitats, opens considerable space, and modifies resources that influence subsequent patterns of colonization. The tissue that remains attached to discarded shells may be an important source of food for several benthic scavengers, including asteroids, ophuiroids, and crustaceans.

Interactions Among Marine Mammals

Walrus may interact trophically with a number of other bottom-feeding marine mammals (Lowry et al. 1980; Lowry and Frost 1981). Gray whales and bearded seals share the walrus' feeding grounds in the Bering and Chukchi Seas, while the sea otter and walrus overlap in the southeastern Bering Sea. Because these other large predators produce a benthic feeding record that is distinct from the walrus, potential interactions can be examined by comparing

[3]F. H. Fay, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. May 1982.

[4]Oliver, J. S., and E. F. O'Connor. Hydraulic excavation of bivalve prey by walrus. Unpubl. manuscr. Moss Landing Marine Laboratories, Moss Landing, CA 95039.

benthic feeding records in areas where the species do and do not overlap.

Walrus and sea otters may compete for food in the southeastern Bering Sea, where sea otters forage extensively in soft-sediment habitats. In contrast to the situation in rocky shores (e.g., Estes et al. 1982), the feeding ecology of sea otters in soft sediments is poorly understood. Along the California coast, sea otters feed on several species of bivalves, including Pismo clams, *Tivela stultorum*; Washington clams, *Saxidomus nuttallii*; and gaper clams, *Tresus nuttallii* (Stephenson 1977; Hines and Loughlin 1980), on tellinid clams *Tellina* sp. in Prince William Sound (G. A. VanBlaricom[5]), and on razor, *Siliqua alta*, and surf, *Spisula polynma*, clams along the Alaska Peninsula (pers. obs.). They excavate pits with the forelimbs and commonly produce sediment piles next to the excavation. Unlike the sea otter, walrus pits do not have piles of extracted sediment. Because otters break shells to extract soft parts, the discarded shells of walrus and sea otters are easily separated as well. Walrus feed along the northeastern portion of the Alaska Peninsula,[6] while sea otters occur more to the southwest. However, their ranges do overlap in the central area. Therefore, feeding records can be quantified in areas of overlap and non-overlap for both species.

Walrus and bearded seals may compete for bivalves in the northern Bering and Chukchi Seas (Lowry et al. 1980). Although we have not observed the benthic feeding record of bearded seals, we predict that it is distinct from the walrus record, and thus amenable to the same sampling scheme outlined for the sea otter-walrus feeding grounds in the southern Bering Sea.

Gray whales do not consume large bivalves, but they may have a negative effect on the walrus food resource by reducing the recruitment or survival of walrus prey. One possible hypothesis is that gray whale feeding kills clams by direct burial, or by clogging feeding structures. We predict that this hypothesis is incorrect. A more likely hypothesis is that gray whale disturbance has a positive influence on several species of amphipod crustaceans, and that these crustaceans decrease the recruitment of young bivalves by predation, trampling, or some less direct interference. This idea can be tested by excluding whales from a bottom area with a large (perhaps 20 × 20 m) canopy made of net on a pipe frame. Walrus feeding probably has little or no effect on gray whales.

This discussion speculates broadly about the usefulness of the benthic feeding record. But much of the speculation can be formulated into hypotheses that are subject to critical tests. Comparable ideas about most other marine mammals, especially the non-bottom-feeding species, are extremely difficult to test, either by manipulative experiments or by sampling natural contrasts. For this reason, the benthic feeding record will undoubtedly make important contributions to our understanding of foraging behavior, community roles, and interactions among marine mammals.

[5]G. R. VanBlaricom, U.S. Fish and Wildlife Service, Piedras Blancas Field Station, P.O. Box 67, San Simeon, CA 93452, pers. commun. December 1981.

[6]Fay, F. H., and F. L. Lowry. 1981. Seasonal use and feeding habits of walruses in the proposed Bristol Bay clam fishery area. North Pac. Fish. Manage. Counc., Doc. 18, 60 p.

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A COMPARISON OF GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, FEEDING IN THE BERING SEA AND BAJA CALIFORNIA

JOHN S. OLIVER, PETER N. SLATTERY, MARK A. SILBERSTEIN, AND EDMUND F. O'CONNOR[1]

ABSTRACT

Our observations indicate that gray whale feeding on benthic invertebrates is rare in the calving lagoons of Baja California and along the open coast near the Scammon's Lagoon complex. The biomass of benthic invertebrate prey is 20 times greater in the northern feeding grounds of the Bering Sea (482 vs. 24 g/m^2). Although the abundance of infaunal invertebrates is only 1.5 times greater in the Bering Sea, most infauna in the calving lagoons are very small polychaetes, bivalves, and crustaceans inhabiting dynamic, coarse sands. The low infaunal abundance and biomass are not caused by gray whale activities in the calving lagoons, as adjacent southern lagoons which are rarely utilized by gray whales have the same infaunal patterns. San Quintin has a unique bottom community which is strikingly different from the more southerly lagoons in Baja California, as well as the northern lagoons in California. Surprisingly, San Quintin shares a number of faunal similarities with gray whale feeding areas in the Bering Sea. No fecal material or bottom excavations made by feeding whales were found in the lagoons of Baja California, including San Quintin. However, the possible expansion of the gray whale population may lead to dramatic changes in the rich bottom communities of San Quintin, and perhaps in shallow water benthic assemblages along the migration route, and in the Gulf of California, which also may harbor potential infaunal prey of gray whales.

Gray whales, *Eschrichtius robustus*, are the only baleen whales that feed primarily on benthic invertebrates (Pike 1962; Rice and Wolman 1971). They consume large numbers of benthic infauna, especially amphipod crustaceans (Zimushko and Ivashin 1980), apparently by ingesting sediment and filtering the infauna on the baleen while expelling sediment and other particles that pass through the baleen fringes (Ray and Schevill 1974). The major feeding grounds are the northern Bering Sea, particularly the central and western regions, and the Chukchi Sea (Bogoslovskaya et al. 1981). Here, the water depths are generally 30 to 40 m and the extensive and shallow continental shelf, the Beringian Platform, supports the largest numbers of bottom-feeding marine mammals in the world. In addition to gray whales, walruses, bearded seals, and sea otters feed primarily on benthic invertebrates in the Bering and Chukchi Seas (Lowry and Frost 1981; Frost and Lowry 1981).

Most gray whales leave the northern feeding grounds in the fall and migrate over 10,000 km to Baja California, where calving occurs in several large, shallow, protected lagoons (Scammon 1874). The whales return to the Bering Sea as the sea ice degenerates in the late spring (Rice and Wolman 1971). Very little feeding is believed to occur outside the northern feeding grounds, as gray whale stomachs are generally empty along the migration route (Scammon 1874; Andrews 1914; Pike 1962; Rice and Wolman 1971), and in the southern lagoons (Scammon 1874). However, feeding has been suggested (Gilmore 1961; Pike 1962; Sund 1974) or documented (Howell and Huey 1930; Mizue 1951; Rice and Wolman 1971) outside the northern feeding grounds on several occasions.

There is additional evidence that gray whale feeding may be relatively common in and near the calving lagoons (Norris et al. in press). In the Bering Sea, many naturalists have observed distinct sediment plumes behind whales that apparently were filtering benthic invertebrates from ingested bottom sediments (Wilke and Fiscus 1961; Pike 1962; Harrison 1979; pers. obs. by authors). Similar sediment plumes or trails have been observed in the calving lagoons (Walker 1975; Norris et al. 1977; Sprague et al. 1978; Norris et al. in press), as well as sediment-laden water passing through the baleen (Norris et al. in press). This behavior suggests benthic feeding similar to that observed in the Bering Sea.

The bottom fauna has not been sampled from any of the lagoons of Baja California, except San Quintin (Barnard 1970). If bottom communities in the calving lagoons are similar to San Quintin, gray whale feeding should be common in Baja California. Laguna San Quintin is located 300 km north of the first calving lagoon, Guerrero Negro, and contains large numbers

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of amphipod crustaceans and polychaete worms (Barnard 1970). In fact, the most abundant crustacean, *Ampelisca agassizi* (*A. compressa* in Barnard 1970), is closely related to *A. macrocephala*, a major prey of gray whales in the Bering Sea (Rice and Wolman 1971). The total abundance of infaunal invertebrates in Laguna San Quintin is as high as 66,700 individuals/m^2 of bottom (Barnard 1970). Although there are no benthic biomass data from San Quintin, the species composition and abundance patterns suggest a significant quantity of potential gray whale prey. San Quintin may have been an important gray whale habitat in the past, and in the last several years has been visited by a few gray whales each season (Sprague et al. 1978).

The recent behavioral observations in the breeding lagoons and the quantity of potential prey in Laguna San Quintin suggest that gray whale feeding on benthic invertebrates may be relatively common in Baja California. If this hypothesis is accurate, perhaps gray whales migrate to the southern lagoons because of the availability of benthic prey, as well as for the warm temperature and protection for calves. Many whales occur at the entrances and outside the calving lagoons where apparent feeding behavior also has been observed (Norris et al. in press). Although we were primarily concerned with bottom communities within the lagoons, lagoon entrances and offshore habitats were explored as well.

Because stomach contents of gray whales are unavailable from recent years, we were unable to examine diets directly. Instead, we compared populations of benthic prey in the Bering Sea with the abundance and biomass of potential benthic prey in San Quintin and five other lagoons of Baja California (three calving and two noncalving lagoons). In addition, we searched the calving and noncalving lagoons for two important signs of gray whale feeding: Benthic feeding excavations and fecal material.

METHODS

Benthic invertebrate communities were surveyed in six coastal lagoons of Baja California during January 1981 (Fig. 1). Laguna San Quintin is the most northerly lagoon and is visited only infrequently by gray whales. There is little or no gray whale activity in Laguna Manuela and Estero Coyote, which are small southern lagoons with shallow entrances and channels. Laguna Guerrero Negro, Ojo de Liebre (Scammon's Lagoon), and San Ignacio are large lagoons and major calving areas for gray whales. The other important calving area, the complex of lagoons around Bahia Magdalena, was not surveyed in the present study (Fig. 1).

The six lagoons were surveyed by divers with and without scuba. Because even the deeper lagoon channels are relatively shallow (often <10 m), bottom communities were surveyed by skin divers without scuba. Scuba was used to collect quantitative samples and to make more detailed observations of areas of special interest. About 40% of the dive areas shown in Figure 1 involved scuba. Each lagoon was surveyed by two sets of divers from two small boats.

Quantitative bottom samples were taken with diver-held corers (0.018 or 0.0075 m^2), washed over a 0.5 mm screen, and preserved in a solution of 4% formaldehyde. Samples were taken in three major habitats: The central channel, eelgrass beds on the channel edges, and unvegetated sandflats above the eelgrass. Most benthic invertebrates were identified to the lowest possible taxon, and wet weight of the total fauna from each core sample was recorded. The

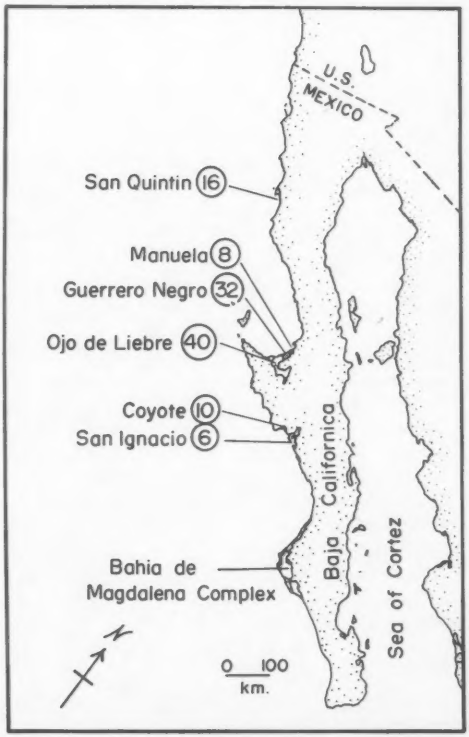

FIGURE 1.—Study sites along the Pacific coast of Baja California. Number of survey dives indicated for each site.

total length of several abundant crustaceans and polychaete worms was measured under a compound microscope with an ocular micrometer. Divers also made numerous visual observations in the relatively clear waters (visibility = 1 to 6 m) and collected qualitative samples of plants and animals.

Benthic invertebrate communities also were surveyed in the central portion of the northern Bering Sea and near St. Lawrence Island from 29 June to 10 July 1980 (Nerini in press) and the northeastern Bering Sea from May to June 1981 (Fig. 2). Water depths varied from 9 to 40 m and bottom-water visibility was generally low, ranging from 0.5 to 3 m. Bottom samples were taken by divers using scuba. The same techniques used to procure and process infaunal and sediment samples in Baja California were employed in the Bering Sea.

RESULTS

Fecal Material

Several fecal slicks were observed floating on the surface waters during the two Bering Sea visits. One large slick was sampled on 10 July 1980 on the southeastern side of St. Lawrence Island (Fig. 2). This region is a feeding ground for gray whales, and earlier bottom sampling documented extensive crustacean communities dominated by the amphipod, *Ampelisca macrocephala* (Stoker 1978, 1981). Although *A. macrocephala* was abundant in the fecal sample (Table 1) and in our bottom samples (see section on Infaunal Prey), a group of large prey, including 10 species of gammaroid and talitroid amphipods (Table 1), did not occur in any of the bottom cores taken in 1980 or 1981 (core number = 156). Gam-

TABLE 1.—Prey items in a gray whale fecal slick collected from the sea surface near St. Lawrence Island, Bering Sea. From triplicate 1,000 ml subsamples.

	Size (mm)	No./1,000 ml
Amphipods		
Gammaroids (6 species)	15-20	176
Ampelisca macrocephala	15-20	154
Talitroids (2 species)	15-20	4
Talitroids (2 species)	5-10	140
Calliopius sp.	5	219
Ischyrocerus sp.	4-8	4,305
Isopods		
Idotheids	10-50	72

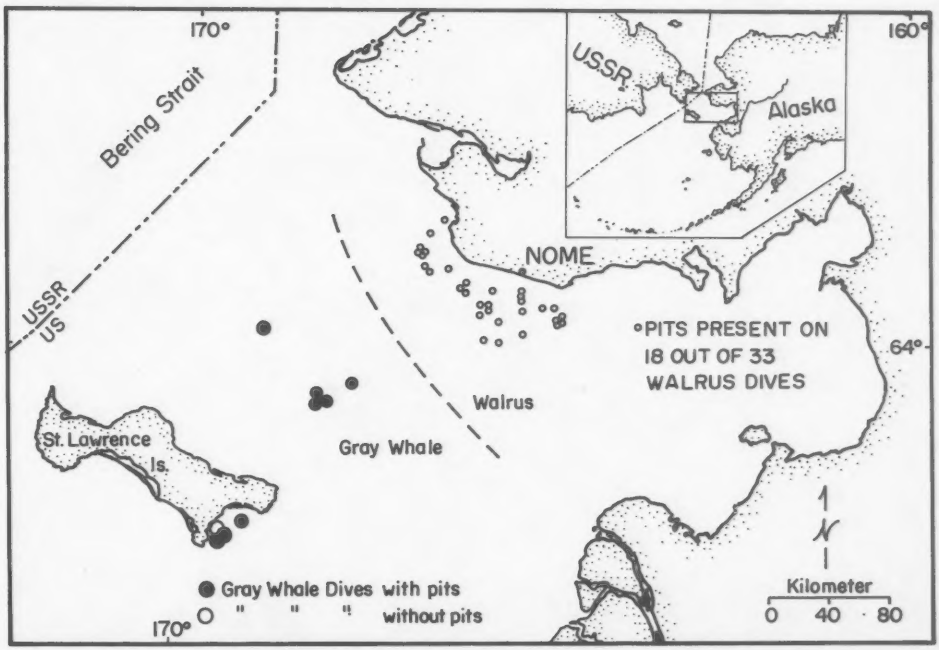

FIGURE 2.—Diving survey stations in the northern Bering Sea. No walrus excavations occurred outside the walrus feeding ground and no gray whale excavations occurred within this area.

maroids and talitroids commonly occur in intertidal, estuarine, and freshwater habitats (Bousfield 1973), and may be nestled among macroalgae in shallow, rocky areas around St. Lawrence Island. These large species (>10 mm) were conspicuous and easily counted without a microscope. Inspection of subsamples of the fecal slick under a dissecting microscope revealed a large number of smaller crustaceans (<5 mm), which were undetected by even the keen observer with the naked eye. The most abundant smaller forms were calliopiid and ischyrocerid amphipods (Table 1), nestlers and tube builders, respectively (Barnard 1969).

We were unable to locate the fecal slicks in the southern lagoons or to find anyone who has seen prey remains in fecal material.

Feeding Excavations

A remarkable record of the feeding activities of gray whales was found in the bottom sediments of the Bering Sea (Fig. 2) (Nerini in press). Divers located many large pits (more than 50) covering as much as 70% of a local bottom area near St. Lawrence Island. Figure 3 is a scale drawing of a less disturbed pitted site observed during another dive. Although we did not observe a whale making an excavation (bottom visibility was about 2 m), a feeding whale is included in Figure 3 for scale. Gray whales and the fecal slick described earlier (Table 1) occurred within 1 km of the site depicted in Figure 3. These large excavations were 1 × 2 m and 0.5 m deep. Most pits had a distinct, oblong, bowl shape. The bottom of many pits contained a deposit of broken bivalve shells (nonliving) that were concentrated from the large volume of ingested sediment. The undisturbed level bottom at the highly pitted site was present only on the ridges between the large excavations. However, a well-developed, dense tube mat of *A. macrocephala* was located on a second dive within 50 m of this highly excavated bottom. Large and small gray whale excavations were encountered on several dives in deeper water (Fig. 2). No gray whale excavations were located on many dives along the eastern shore,

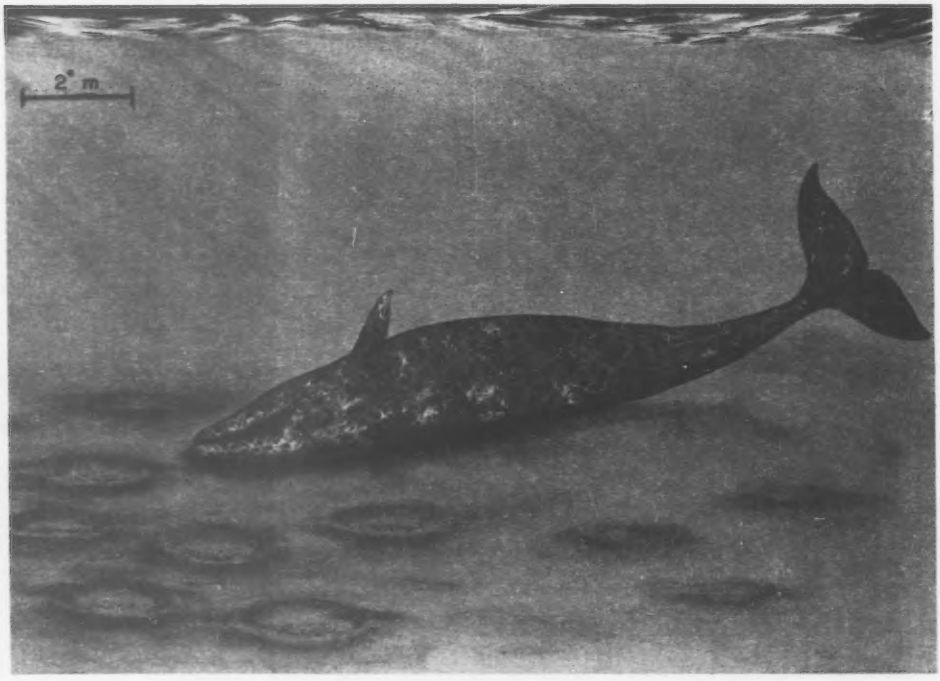

FIGURE 3.—A scale drawing of a heavily excavated bottom area observed by divers near St. Lawrence Island (21 m). No feeding whale was seen here, but a whale is included in the drawing for scale. (Drawn by Sandy Strause.)

where walrus feeding excavations were common (Fig. 2) (Oliver et al. 1983).

No gray whale feeding excavations were observed in Baja California, despite a large number of survey dives (Fig. 1) and better water clarity than the Bering Sea. Although the currents were relatively strong in many of the lagoons, other excavations and sediment structures were maintained in the surface sediments. For example, a large number of excavations produced by feeding rays was observed. These pits persisted in a number of lagoon habitats, but were usually found in the intertidal and shallow subtidal areas where gray whales did not occur. Rays were observed creating pits on several occasions. Qualitative bottom samples commonly revealed large bivalves, especially *Chione* spp., in areas where ray pits occurred. Dense infauna and other patches of potential gray whale prey did not occur in the ray feeding areas.

Infaunal Prey

The abundance of infaunal invertebrates in the gray whale feeding grounds of the Bering Sea was only 1.5 times greater than the total abundance of animals in the calving lagoons, which included Guerrero Negro, Ojo de Liebre, and San Ignacio (Fig. 4). However, ampeliscid amphipods were never abundant in the calving lagoons, while *A. macrocephala* dominated the Bering Sea fauna (also see Neiman 1963 and Stoker 1978). The abundance of infaunal crustaceans and *A. macrocephala* in the gray whale feeding grounds (Fig. 2) was as high as 67,746/m^2 and 21,448/m^2, respectively. Infaunal abundance was highest in San Quintin, the most northerly lagoon surveyed in Baja California (Fig. 4). Here we sampled from dense beds of *A. agassizi*, which accounted for 95% of the total individuals and occurred in abundances as high as 135,912/m^2.

In contrast to abundance, the biomass of the infauna was 20 times greater in the Bering Sea than in the calving lagoons (Fig. 5). Over 70% of the biomass in San Quintin was *A. agassizi*, and the total biomass was more than half of the Bering Sea value (Fig. 5). However, the Bering Sea data were averaged over a large group of stations sampled by Stoker (1978). The value shown for San Quintin was the densest *Ampelisca* bed we observed.

Most of the benthic invertebrates living in the southern lagoons were quite small. This was clearly reflected in the biomass data (Fig. 5). In addition to the rarity of large species and individuals, deposit feeders also were relatively rare among the polychaete worms, especially in the unvegetated sedimentary habitats. For example, a suspension-feeding sabellid worm (probably *Fabricia)* was the only species that occasionally occurred in relatively high abundance (maximum of 250 in a 0.0075 m^2 core). This species was usually <5 to 6 mm long, and

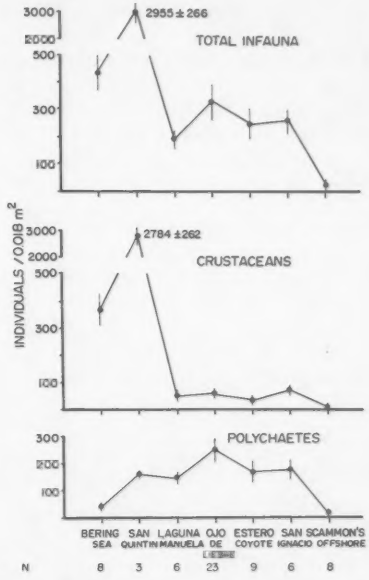

FIGURE 4.—Abundances of total infaunal invertebrates, crustaceans, and polychaete worms in the gray whale feeding grounds of the Bering Sea and in Baja California. Means and standard errors.

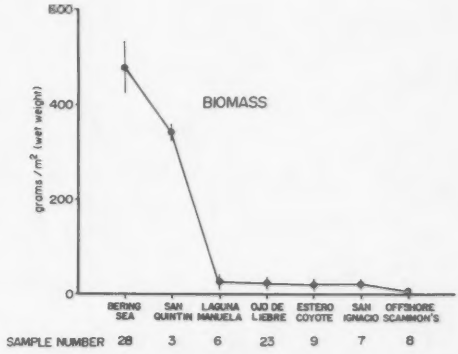

FIGURE 5.—Wet weight biomass of the total infauna from the gray whale feeding grounds in the Bering Sea (from Stoker 1978) and in Baja California. Means and standard errors.

accounted for the relatively high abundance of polychaetes in Ojo de Liebre (Fig. 4). The few infaunal crustaceans (Fig. 4) also were small species and individuals <6 mm in length vs. 20 mm for typical Bering Sea individuals). Although *A. agassizi* was a relatively large benthic crustacean for the lagoons of Baja California, this species was much smaller than *A. macrocephala* from the Bering Sea (Fig. 6).

Samples from the channel and eelgrass habitats in each lagoon were lumped for Figures 4 and 5, but infaunal abundance and biomass were highest in the eelgrass beds. When Laguna Manuela and Estero Coyote were considered together with the three calving lagoons (Fig. 1), the overall infaunal biomass was 24.3 ± 0.9 g/m² ($\pm$ SD; $n = 45$). Infaunal biomass in eelgrass habitats was 35.9 ± 2.7 g/m² ($n = 21$) and was only 13.2 ± 1.6 g/m² ($n = 24$) in the channels. This difference was highly significant ($P < 0.001$; Mann Whitney U test).

All the lagoon entrances were surveyed in the present study except San Ignacio. Qualitative sampling of the infaunal and epifaunal invertebrates revealed very low numbers and biomass. Quantitative core samples taken at the entrance of Laguna Ojo de Liebre substantiated these observations (only 14 g/m²).

The biomass of potential benthic prey was extremely low outside the lagoon entrances as well. Benthic invertebrate communities were surveyed outside the Scammon's Lagoon complex between Laguna Manuela and Guerrero Negro (Fig. 1). The infauna were sampled at two water depths (9 and 17 m) and in areas that were likely to harbor well-developed infaunal populations. The substrate was a coarse, mobile sand at each depth. When the depths were combined, the infaunal biomass was 2.7 ± 3.3 g/m² (SD; $n = 8$). This was considerably lower than the low biomass recorded from the lagoon channels ($P < 0.0001$; Mann Whitney U test). A dense concentration (100-200/m²) of the heart urchin, *Lovenia cordiformis*, was not included in the biomass figures because this species is not a potential prey for gray whales. Our experiences along other wave-exposed coasts (Oliver et al. 1980) indicate that unobserved patches of dense infaunal prey probably do not occur in offshore habitats.

No large zooplankton, including euphausiids and galatheid crabs, were seen by divers in the offshore habitats, in the lagoons, or in the lagoon mouths (Norris et al. in press).

In addition to the plankton, conspicuous mobile epifauna were not abundant at the lagoon entrances or anywhere in the lagoons, either on reefs or over the soft sediments. Several groups of the mysid crustacean, *Mysidopsis californica*, were observed near eelgrass beds, but these patches were rare, covered a relatively small area (10 to 20 m²), and did not contain a large number of individuals. Small groups of shrimp were even rarer.

The calving and adjacent noncalving lagoons in the southern part of Baja California had highly dynamic sedimentary environments. We observed tidal currents of 2 to 3 kn in several lagoons. Sediments were primarily coarse sand and gravel (see Phleger and Ewing 1962), and surface structures indicated highly mobile substrates. These structures included broken shell debris and ripple marks as large as 1 m in height. Surprisingly, these structures were not restricted to the lagoon mouth. For example, large lunate ripples (length about 10 m, height 30 cm) occurred in the channel of Estero Norte, an arm of the extreme back lagoon in Ojo de Liebre. These ripple marks were more than 10 m wide, were highly mobile, and changed direction with the tide. Unlike the more southerly lagoons, we encountered relatively fine sands and silts in San Quintin. Similar differences between the sedimentary habitats in San Quintin

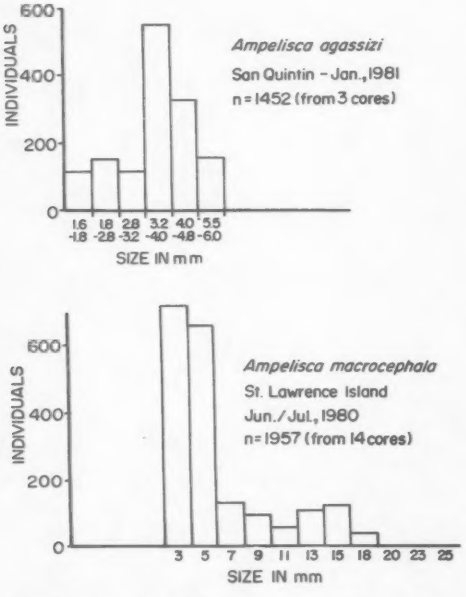

FIGURE 6.—Length-frequency histograms of *A. macrocephala* collected from a variety of stations in the Bering Sea and of *A. agassizi* from San Quintin. *Ampelisca macrocephala* populations were dominated by recently released young in summer samples (molt stages I and II). Most *A. agassizi* were preadult individuals from a midwinter population.

(Gorsline and Stewart 1962) and Ojo de Liebre (Phleger and Ewing 1962) were observed in earlier studies. The Bering Sea areas, like San Quintin, contained less mobile fine sands (Nelson 1982) harboring many relatively large infauna in tubes and burrows (Stoker 1978).

DISCUSSION

The absence of fecal material, benthic feeding excavations, and significant quantities of potential gray whale prey suggest that gray whale feeding on benthic invertebrates is not common in Baja California. No evidence of benthic feeding was encountered within the calving and noncalving lagoons, at lagoon entrances, and along the offshore sand bottoms. Gray whale stomachs collected in the southern lagoons also contained no benthic prey (Scammon 1874; Rice and Wolman 1971).

In contrast to Baja California, there is considerable evidence of gray whale feeding in the northern Bering Sea. Stomach contents are dominated by benthic infauna, especially a few species of large amphipod crustaceans (Table 2). Crustacean communities are well developed in the central and western portion of the area (Neiman 1963; Stoker 1978), the major gray whale feeding grounds. The Russian literature reports a benthic biomass of almost 1,000 g/m^2 in the feeding grounds (Neiman 1963; Alton 1974), and Stoker (1978) found a range from 149 to 991 g/m^2. Over 90% of the biomass was crustaceans, especially *A. macrocephala* in the central basin. Although we only located a few fecal slicks in the Bering Sea, benthic feeding excavations were common.

All the large benthic excavations observed in this study were undoubtedly created by feeding gray whales. Other likely explanations for their origin can be excluded. There are few bottom-feeding fish such as rays or skates in the northern Bering Sea (Shmidt 1950; Wilimovsky 1974). These fish produce large pits in other habitats (Howard et al. 1977; Gregory et al. 1979; VanBlaricom 1982). The abundant bottom fish are in the cottid family (Wilimovsky 1974) and are relatively nondestructive bottom feeders (pers. obs.). One other bottom-feeding marine mammal, the walrus, occurs in the gray whale feeding grounds, but walrus produce entirely different bottom excavations than gray whales (Oliver et al.[2]). We know of no other likely biological explanation for the large pits.

Two physical processes produce large excavations on the sea floor, ice gouging and biogenic gas cratering. Although ice gouging produces deep excavations in the sea floor (Reimnitz et al. 1977), this scour does not produce regular, bowl-shaped depressions and usually causes much more extensive bottom disturbance (Reimnitz et al. 1977; Larsen et al. 1981; Thor and Nelson 1981; pers. obs. by authors). Release of biogenic gas from the sediment apparently produces large craters in Norton Sound, and several other areas with gas-producing strata, but not in the gray whale feeding grounds (Nelson et al. 1979).

Gray whale feeding excavations can be easily distinguished from the benthic feeding record of walrus (Oliver et al. 1983). Walrus excavations were common along the eastern shore, and gray whale excavations only occurred in the central study area (Fig. 2). Here, the gray whale prey (Stoker 1978) and feeding gray whales (Moore and Ljungblad in press) are much more abundant. Gray whales are infrequently encountered along the eastern shore, where bivalve

[2]Oliver, J. S., P. N. Slattery, M. A. Silbertstein, and E. F. O'Connor, 1983. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Unpubl. manuscr. Moss Landing Marine Laboratories, Moss Landing, CA 95039.

TABLE 2.—Dominant prey species contained in gray whale stomachs. All are benthic and all but *Synidotea* sp. are amphipods. Stomachs usually contain one prey species which comprises 80 to 100% of total contents (Zimushko and Lenskaya 1970; Bogoslovskaya, et al. 1981).

Prey species	Number stomachs dominated by prey species					
Ampelisca macrocephala	12	11	1	1	[1]	[1]
Pontoporeia femorata	23	10				
Atylus spp.	7	1			[1]	
Anonyx nugax	10					
Byblis gaimardi		4				
Ampelisca eschrichti	1					
Synidotea sp.	1					
Source	Zimushko and Ivashkin 1980	Bogoslovskaya et al. 1981	Coyle unpubl. manuscr.[2]	Pike 1962	Zenkovich 1934	Tomlin 1957

[1]Dominant species where number of stomachs examined were unreported.
[2]Coyle, K. O. 1981. The oceanographic results of the cooperative Soviet-American cruise to the Chukchi and East Siberian Seas aboard the Soviet whale hunting ship Razyashchii, Sept.-Oct. 1980. Unpubl. manuscr. University of Alaska, Institute of Marine Science, Fairbanks, AK 99701.

molluscs dominate the benthic biomass. The separation of the feeding grounds of gray whales and walrus can be documented by side-scan sonar, which clearly relates general changes in surface sedimentary structures to the large-scale feeding activities of gray whales and walrus.[3] When properly calibrated with in situ observations, individual feeding excavations and multiple excavation patterns (footnote 2) may be accurately interpreted on side-scan sonographs (pers. obs. by authors).

Gray whales also produce benthic feeding excavations along Vancouver Island in British Columbia (footnotes 3, 4). Fecal material has been collected along this coast as well.[5] We recently discovered dense beds of ampeliscid amphipods and an extensive benthic feeding record of gray whales near the Bamfield Marine Station (see footnote 2). Many whales apparently feed along Vancouver Island during the northward migration, and some individuals spend the entire summer here (Darling 1977).

In summary, despite considerable evidence of benthic feeding in northern habitats, there is no compelling evidence for benthic feeding in or near the lagoons of Baja California. The southern lagoons contain highly dynamic, coarse sediment harboring very small infauna and little prey biomass for gray whales. Most infauna are much smaller than the spaces between the gray whale baleen. The structure of benthic communities within the calving lagoons is not influenced by gray whale activities, because bottom communities in adjacent noncalving lagoons are similar to those in the calving lagoons.

Earlier studies of the gray whale diet imply highly selective feeding on large crustaceans (e.g., Pike 1962). While two species of large amphipods, *Pontoporeia femorata* and *A. macrocephala*, generally account for much of the prey biomass (Table 2), careful examination of the prey remains in a fecal slick revealed a surprisingly large number of smaller prey. Gray whales probably are relatively nonselective filter feeders, consuming most of the large and small infaunal forms. Despite the importance of benthic prey, gray whales are clearly opportunistic feeders, consuming both large and small benthic invertebrates, epifaunal invertebrates in kelp forests (Wellington and Andersen 1978) and along rocky shores (see footnote 2), zooplankton (Rice and Wolman 1971; Norris et al. in press), and fish (Gilmore 1961; Sund 1975).

Although some observations of apparent feeding behavior in the breeding lagoons undoubtedly involve planktonic feeding (Norris et al. in press), and opportunistic consumption of some benthic animals, much of this behavior probably results in little or no food. A number of other explanations are likely. For example, a local fisherman and naturalist, Mario Rueda, directed us to a specific habitat near Piedras Island in Ojo de Liebre, where apparent feeding behavior was consistently observed. This area contained no concentrations of potential infaunal or epifaunal prey. However, the bottom relief was spectacular. Rocky outcrops formed a series of parallel ridges much like giant and stable ripple marks on the bottom. The vertical relief was 2 to 3 m. Between the rocky crests, there were deep basins where water currents were very low. The distance between crests was 5 to 10 m. The tidal currents above these ridges were extremely strong. Perhaps gray whales are attracted to this current regime where individuals can rapidly swim in and out of mild and strong currents over an undulating bottom.

Laguna San Quintin contains a unique bottom community, which is strikingly different from the lagoons of California and the five lagoons that were surveyed in central and southern Baja California. San Quintin harbors a large number of potential gray whale prey in a relatively small area. Future expansions of the gray whale population may bring more whales to San Quintin. If the whales arrive and do not avoid the lagoon because of human activities, we predict a dramatic change in the bottom communities of San Quintin. A small group of whales might spend much of the winter and spring feeding in San Quintin. Like the relatively small feeding areas along the coast of British Columbia, San Quintin could become a regular stopping place for certain individuals. There may be equally suitable areas for feeding around the Gulf of California, where gray whales were known to breed in the past (Gilmore et al. 1967). While these local patches of prey may be unimportant to the entire population, they may become important to certain individuals. Relatively few feeding gray whales could have considerable effects on local benthic habitats, and could produce long-term patterns of bottom population and community change.

ACKNOWLEDGMENTS

We are very grateful for the considerable support of Lloyd Lowry, Robert Nelson, and Kathy Frost (Alas-

[3]Hans Nelson and Kirk Johnson, U.S. Geological Survey, Menlo Park, CA 94025, pers. commun. August 1982.

[4]J. Hudnall showed underwater slides and a movie of feeding excavations and behavior at the 4th Biennial Conference on the Biology of Marine Mammals, San Francisco, Calif., December 14-18, 1981.

[5]J. Darling reported, at the 4th Biennial Conference on the Biology of Marine Mammals in San Francisco, Calif., December 14-18, 1981, that K. Norris and students collected this sample near the Bamfield Marine Station, British Columbia.

ka Department of Fish and Game). Luis Fleisher and his collegues kindly helped provide access to the calving lagoons (Permiso No. 2 de Investigacion Cientifica, 1981). The field work in Baja California depended on our coworkers, James Oakden and Linda Martin. Paul Dayton, Glenn VanBlaricom, and Lloyd Lowry introduced us to the feeding ecology of gray whales and stimulated many ideas. Sheila and Alan Baldridge generously contributed to almost all aspects of our studies. Sandy Strause and Lynn McMasters drew the figures and Rosie Stelow typed the manuscript. The American Cetacean Society, World Wildlife Fund, and National Science Foundation (DPP 8121722) provided essential funds and encouragement. Collection of the 1980 Bering Sea data was funded by the Outer Continental Shelf Environmental Assessment Program, Juneau Project Office (principal investigators Mary Nerini, Howard Braham, and Linda Jones, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, Wash). The manuscript was improved by comments from Glenn VanBlaricom, Bernd Wursig, and Kathy Frost.

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ANALYZING THE WIDTH OF DAILY OTOLITH INCREMENTS TO AGE THE HAWAIIAN SNAPPER, *PRISTIPOMOIDES FILAMENTOSUS*

STEPHEN RALSTON[1] AND GARRET T. MIYAMOTO[2]

ABSTRACT

Studies of otolith microstructure in Hawaiian snapper, *Pristipomoides filamentosus*, indicate that growth increments are deposited daily in immature fish (<40 cm FL and <3 yr of age). Laboratory experiments with tetracycline-injected fish and analysis of modal progression in size-frequency distributions of field-sampled fish validate this conclusion. Given a 1:1 correspondence between increments and days, one can determine otolith growth rate by measuring increment width. Based on the relationship between otolith growth rate and otolith length, we conclude that increment deposition in mature *P. filamentosus* is episodic, i.e., interrupted.

Using regression analysis, a model is developed relating otolith growth rate to otolith length. It is shown that integration of the regression equation provides estimates of the age of individual fish. Assumptions involved in the model are discussed, and it is concluded that this method of aging adequately represents the growth of *P. filamentosus* when time is measured on a scale of years. Age estimates derived here are entirely consistent with those of related forms (Lutjanidae) reported in the literature.

Studies of fish otoliths have now revealed that these calcified structures often grow by daily accretion of increments, in a manner analogous to the annual rings of trees. Pannella (1971, 1974) was the first to demonstrate this, and now many other researchers have substantiated and extended his findings to a wide variety of temperate and tropical species in both marine and freshwater environments (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Le Guen 1976; Ralston 1976; Timola 1977; Taubert and Coble 1977; Barkman 1978; Brothers 1978; Methot and Kramer 1979; Dunkelberger et al. 1980; Pannella 1980; Schmidt and Fabrizio 1980; Steffensen 1980; Wild and Foreman 1980; Wilson and Larkin 1980; Worthmann 1980; Brothers and McFarland 1981; Mugiya et al. 1981; Uchiyama and Struhsaker 1981; Tanaka et al. 1981; Ralston and Miyamoto 1981; Campana and Neilson 1982; Watabe et al. 1982; Radtke and Dean 1982; Radtke[3]). Daily growth structures from a wide variety of plant and animal tissues were known for some time prior to Pannella's discovery (Choe 1963; Neville 1967). In fact, several publications which predate his work presented photographs of otoliths in which typical daily increments are evident (Hickling 1931; Morris and Kittleman 1967; Degens et al. 1969), yet their temporal significance was unappreciated at the time.

We are now developing a more sophisticated understanding of the processes which control the incremental growth of otoliths, with multiple factors influencing accretion, including photoperiod, food, and temperature (Hickling 1931; Irie 1960; Degens et al. 1969; Mugiya 1974, 1977; Taubert and Coble 1977; Brothers 1978; Dunkelberger et al. 1980; Pannella 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; but see Campana and Neilson 1982). Furthermore, some studies have revealed the existence of subdaily increments (Taubert and Coble 1977; Brothers 1978; Pannella 1980; Wilson and Larkin 1980; Campana and Neilson 1982) which complicates considerably the temporal interpretation of increment periodicities.

A powerful application of daily increment research has been the use of increment width as a measure of otolith and somatic growth rate. Pannella (1974) first presented this view when he stated, "Increment thickness is the spatial expression of time" and "... is the faithful expression of the conditions and rate of growth." In substantiating this claim, Struhsaker and Uchiyama (1976), Taubert and Coble (1977), and Barkman (1978) showed that otolith ring counts depend purely on specimen age and not otolith size. Slow-growing fish had small otoliths, while in comparably aged fast-growing fish the otoliths were larger but contained no more increments. Moreover, Wild and Foreman (1980) used the change in otolith dimension subsequent to mark-

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[3]Radtke, R. L. Scanning electron microscope observations of daily increments and structure in otoliths of the adult tropical fish *Pristipomoides filamentosus*. Manuscr. in prep. Pacific Gamefish Foundation, P.O. Box 25115, Honolulu, HI 96825.

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ing to estimate change in fish length and, ultimately, somatic growth rate. Similarly, Brothers et al. (1976) and Methot and Kramer (1979) numerically integrated increment thickness data to estimate age. Although of some significance, no formal or detailed treatment of the subject was presented. More recently Methot (1981) has measured the widths of the outer three daily increments in the otoliths of larval fishes, using them as explicit measures of recent daily growth rate. Brothers (1981) discussed this kind of application and cautions against short-term uncouplings of otolith growth with changes in fish length.

In this paper, we intend to analytically formalize the concept that increment width can be used as a measure of otolith growth rate. This eliminates the constraint of having to count all increments in an otolith, providing a framework for studying age and growth in large, slow-growing species of fish in which increment microstructure frequently becomes ambiguous with age (Brothers 1979; Pannella 1980). Rather than attempting a numerical solution to this problem, we have analytically integrated increment growth-rate data obtained from the otoliths of Hawaiian snapper, or opakapaka, *Pristipomoides filamentosus* (Lutjanidae). This is a commercially important species of bottomfish harvested in the Hawaiian deep-sea handline fishery (Ralston 1981; Ralston and Polovina 1982). While admittedly sacrificing some of the extreme precision theoretically possible with daily increments, the intent here is to provide reasonably reliable age estimates, economically obtained, when age is measured on a scale of years. Preliminary results of this research have been reported elsewhere (Ralston and Miyamoto 1981).

METHODS

Marking Experiment

A marking experiment was done to validate the existence of daily growth increments in opakapaka. Otoliths are composed primarily of the aragonitic crystalline form of calcium carbonate in association with small amounts of otolin protein (Hickling 1931; Irie 1960; Degens et al. 1969). The presence of calcium carbonate allows otoliths to be successfully marked in vivo with the antibiotic tetracycline (Blacker 1974; Wild and Foreman 1980; Campana and Neilson 1982). A dated, visible time-mark in otoliths provides direct validation of the periodicity of presumed daily increments.

Six juvenile opakapaka (30-34 cm FL (fork length)), captured by hook and line, were acclimated to a 1,135 l flowthrough aquarium. The fish were exposed to a natural photoperiod through an overhead skylight and were fed to satiation twice daily (midmorning and late afternoon). All six fish were initially in good condition, and after 12 d they appeared well adjusted to the tank, having resumed what seemed to be normal feeding behavior.

Three 1 kg specimens were injected intraperitoneally with 30 mg of oxytetracycline (dosage from A. Wild[4]). Following injection, all six fish were exposed for 18 h to 125 ppm acetazolamide in seawater (dosage from J. Dean[5]). This compound has been shown to affect otolith calcification by inhibition of carbonic anhydrase (Mugiya 1977), providing a simple means of creating a checkmark on otoliths. The fish resumed feeding 2 d after treatment. One fish jumped out of the tank 27 d later, and the experiment ended prematurely when the remaining five specimens died unaccountably 38-39 d after treatment.

Preparation of Otoliths

All otoliths in this study were prepared for viewing as outlined in Ralston and Miyamoto (1981). Thin sections (0.5 mm) were made through the focus along a frontal plane to the most distal portion of the postrostrum (Figs. 1, 2). Preliminary observations showed that increment counts made in a transverse plane were less than those made from frontal sections, presumably due to pinching and coalescing of rings along the shorter transverse axis (Pannella 1974; Taubert and Coble 1977; Dunkelberger et al. 1980). Tetracycline marks were obliterated by the clearing agent (Euparal[6]) and were located prior to etching by viewing with an ultraviolet fluorescence microscope. In addition, several otoliths were prepared for scanning electron microscope (SEM) examination.

Otolith Growth Rate and Specimen Age

After otoliths had cleared, they were read with a compound binocular microscope using transmitted light at a magnification of 400×. The distance in microns (μm) between the focus and the postrostral margin, representing the total length (L) of the otolith along the postrostral radius, was measured with a

[4]A. Wild, Inter-American Tropical Tuna Commission, La Jolla, CA 92037, pers. commun. May 1980.
[5]J. Dean, Professor, Belle Baruch Institute, University of South Carolina, Columbia, SC 29208, pers. commun. May 1980.
[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

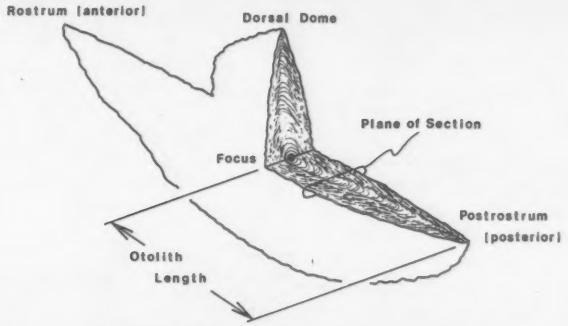

FIGURE 1.—Schematic of an otolith from *Pristipomoides filamentosus* with specific points of reference discussed in the text.

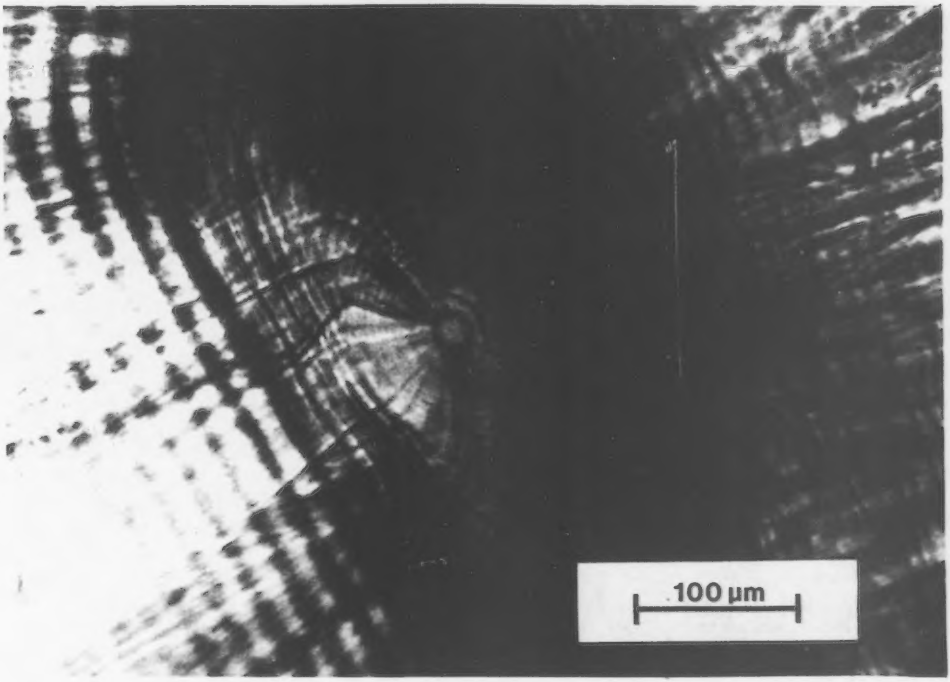

FIGURE 2.—Photomicrograph through the nuclear core region of an otolith from *Pristipomoides filamentosus*. Note increments become compressed in this area.

calibrated ocular micrometer (Fig. 1). Readings were then made at selected points along the postrostral growth axis, wherever increment microstructure was clearly viewed. At such locations the average width of increments was determined by counting the number of increments visible ($\bar{x} = 15.95$, SD = 11.24) and by measuring the radial length of the short segment in which the increments were observed. In addition, the distance between the midpoint of the sample region and the otolith focus (ℓ) was measured along the

same postrostral growth axis. As many readings as possible were made from each preparation ($\bar{x} = 31.9$), subject to the constraint that counts be made only in regions where increments were clear.

Data were summarized for each specimen by computing the ratios of segment length in μm to the number of increments included at each specific segment examined in the preparation. These figures represent the average increment width at given points in the otolith. Under the assumption that one increment forms each day, it is possible to approximate the otolith growth rate on a size-specific basis as follows:

$$\frac{\Delta \ell}{\Delta \text{ increments}} = \frac{\Delta \ell}{\Delta t} \simeq \frac{d\ell}{dt}$$

where $\Delta \ell$ is the change in length (μm) of the otolith over a given subregion, and Δt is the change in time (days). The finite approximation to the differential was always computed on a sufficiently small scale of time and length.

Given the series of ordered pairs, $\frac{d\ell}{dt}$ at otolith length ℓ, it is possible to evaluate the functional relationship between these quantities, $\frac{d\ell}{dt} = f(\ell)$, and to estimate the parameters of the function using regression analysis. The regression equation can then be solved by separation of variables and treated as a definite integral, bounded by the focus and the total length (L) of the otolith at death, providing an explicit estimate of age in days (T). That is:

$$\int_{t=0}^{T} dt = \int_{\ell=0}^{L} [f(\ell)]^{-1} d\ell. \qquad (1)$$

Size at Maturity

Samples of opakapaka gonads were obtained from throughout the Hawaiian Archipelago. Sampling was haphazard with respect to both time and location. Gonads were preserved in 10% Formalin until examined, when they were weighed to the nearest gram after excess moisture had been removed by blotting with a paper towel. Sex was determined by microscopic examination of smeared gonadal tissues, and ovaries were staged according to the following classification:

Stage I. Inactive ovary
- a) egg diameters 75-100 μm
- b) transparent primary oocytes in ovary
- c) nucleii faintly visible
- d) eggs ovoid

Stage II. Developing ovary
- a) egg diameters 100-325 μm
- b) some opaque eggs in ovary
- c) nucleii clearly visible
- d) eggs wedge-shaped

Stage III. Gravid/spawning ovary
- a) egg diameters 325-850 μm
- b) presence of oil globules
- c) evidence of yolk granules
- d) eggs ovoid

RESULTS

Typical looking increments are found in the sagittae of opakapaka (Fig. 3). In this SEM photograph the distinct incremental growth of the otolith is readily apparent, with a structure similar to that described in previous descriptions of daily increments. Discernible under high magnification is a more deeply etched, discontinuous zone which transects the radial growth of aragonite crystals found in the incremental zone (Hickling 1931; Pannella 1971, 1974, 1980; Blacker 1975; Brothers et al. 1976; Timola 1977; Dunkelberger et al. 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; Radtke footnote 3).

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Photomicrographs of a sagittal section through the otolith of one of the three experimental fish injected with oxytetracycline are presented in Figure 4. In the upper photograph the specimen was illuminated with ultraviolet light, clearly showing the fluorescing tetracycline checkmark. The lower photograph shows the same specimen illuminated with visible light. A discontinuity coincident with the tetracycline label is evident. We interpret this latter checkmark to be due to exposure to acetazolamide and handling trauma. The close coincidence of the two marks allowed us to positively identify the experimentally induced checkmark in all six specimens.

The results of marginal increment counts from these fish are summarized in Table 1. Several sections were taken from each otolith, although not all preparations were readable. Furthermore, because the quality of all sections was poor, multiple counts of each section were made. The figures under the heading "Number of marginal increments" represent the range of counts.

It is evident from these data that the number of increments deposited on the otoliths after marking was quite similar to the number of days elapsed after the fish were marked. Since these fish were stressed dur-

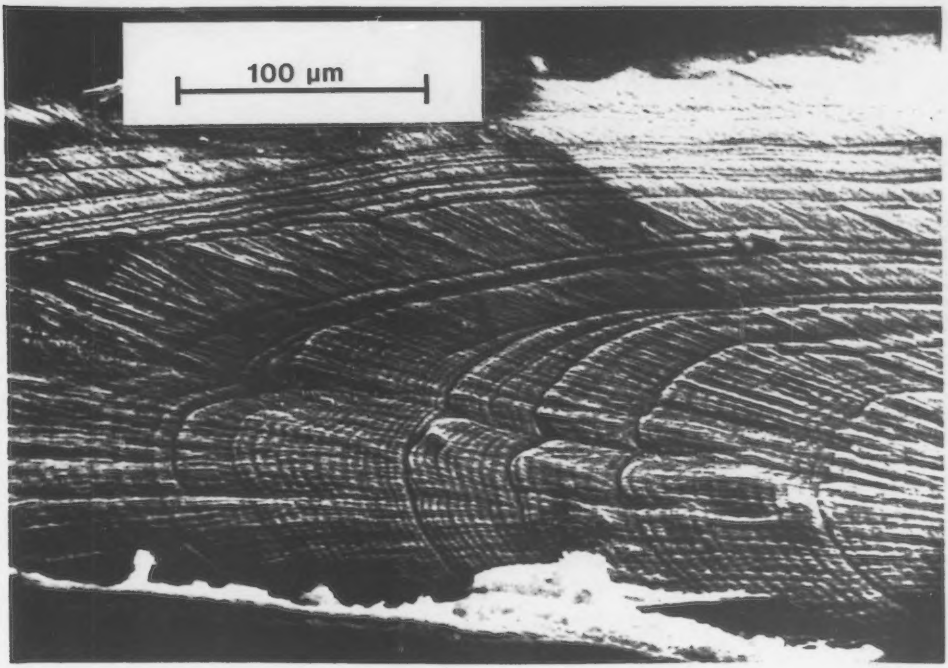

FIGURE 3.—A scanning electron microscope (SEM) photograph of a sagitta from *Pristipomoides filamentosus*, showing radial development of aragonite crystals transected by incremental and discontinuous zones.

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Otolith Growth

Due to the likelihood of allometric relationships, it is important to distinguish between the growth of the otolith and the growth of the whole fish. Figure 5 shows that the slope of the log-linear power function regression of otolith length on fork length, based on measurements from 66 individuals, is significantly <1 ($\beta = 0.6286, t = -14.12, \mathrm{df} = 64$). This is typical of many fish species (Hickling 1933; Templeman and Squires 1956; Blacker 1974; but see Taubert and Coble 1977) and implies that the growth rate of opakapaka otoliths $\left(\frac{d\ell}{dt}\right)$ is not related in a simple linear fashion to somatic growth rate.

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E-1, Section D	27	24-27
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Section C		35-38
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E-4, Section A	38	30-32
Section B		30-38
E-5, Section A	38	37-39
Section C		30
E-6, Section C	39	27-30
Section D		35-39

A total of 81 sagittae from 68 individuals were examined with light microscopy for presence of daily increments. In 13 cases both left and right otoliths from the same individual were viewed. These 81 samples provided 2,957 separate estimates of otolith growth rate along the postrostral growth axis. Initially the data were pooled to elucidate the functional relationship between otolith growth rate and otolith length. The results are presented in Figure 6.

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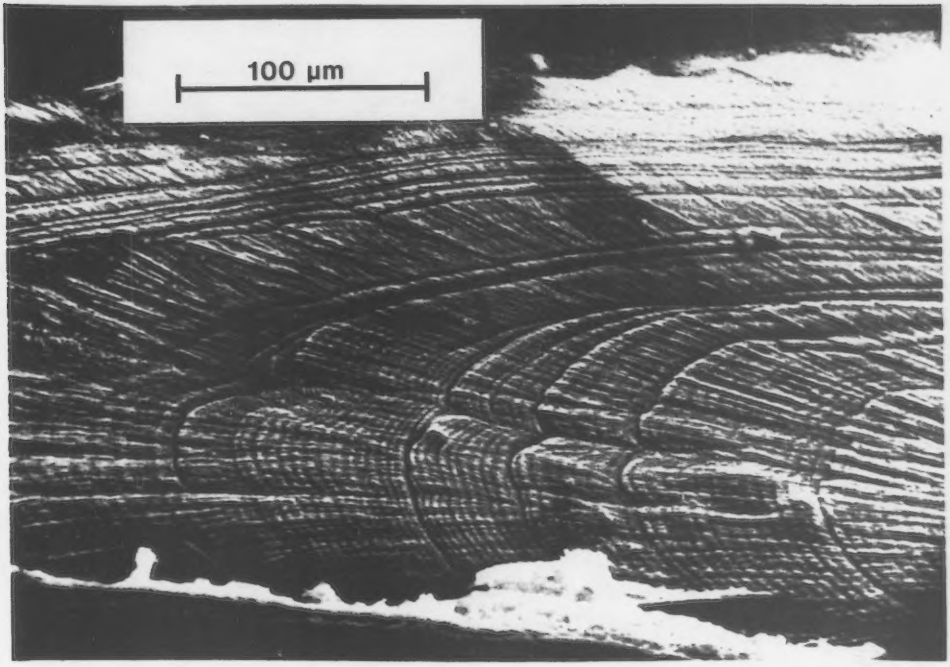

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FIGURE 4.—(top) Photomicrograph of a tetracycline-marked otolith of *Pristipomoides filamentosus*, illuminated by ultraviolet light. Note checkmark at arrow. (bottom) Photomicrograph of the same sample illuminated under visible light. 300× magnification.

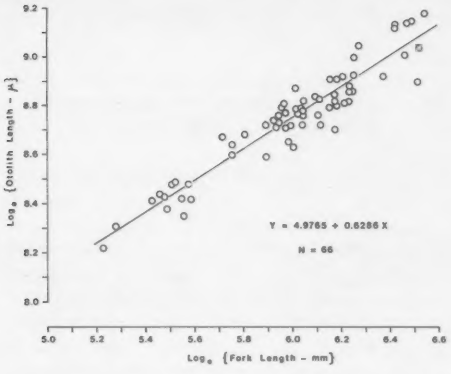

FIGURE 5.—Relationship between otolith length and fork length in *Pristipomoides filamentosus*.

There is pronounced curvilinearity in the data, as well as heteroscedastic variance. The von Bertalanffy growth model (Ricker 1979) asserts that somatic growth rate in length is a linear decreasing function of length, with the X-intercept defining the asymptotic upper bound on growth (L_∞). The observation that the growth-rate curve of opakapaka otoliths is a concave (upwards), monotonic decreasing function of otolith length (Fig. 6) is consistent with this notion, given the previously deduced allometric relationship between fork length and otolith length.

Growth-rate data were logarithmically transformed to linearize the trend line and stabilize the variance (Fig. 7). It is evident that once the otolith reaches about 6,000 μm in length, an alteration occurs in the rate (slope) at which log-transformed growth rate declines, maintaining a higher rate than would be expected otherwise. This noticeable change in slope is apparently due to attainment of reproductive maturity.

Of those female opakapaka collected during the summer spawning season (Kikkawa 1980; Ralston 1981), the incidence of gravid/spawning ovaries is strongly dependent upon fish size (Fig. 8). These data indicate that female opakapaka reach reproductive maturity at about 40 cm FL. Fish this length have otoliths about 6,250 μm long (Fig. 5). Thus the distinct change in trend of otolith growth rate coincides closely with maturation. Males show a similar pattern of gonad maturation (Ralston 1981).

Based on these observations, it is likely that periods of episodic growth commence in opakapaka otoliths with the onset of maturity. That growth dynamics should improve at this time, as suggested by a moderation in the decline of log-transformed otolith

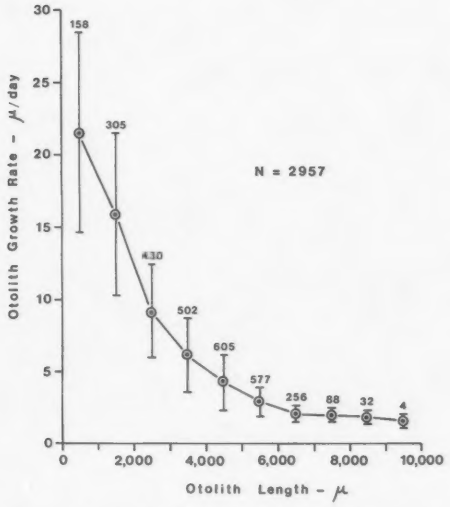

FIGURE 6.—Relationship between otolith growth rate (increment width) and otolith size in *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

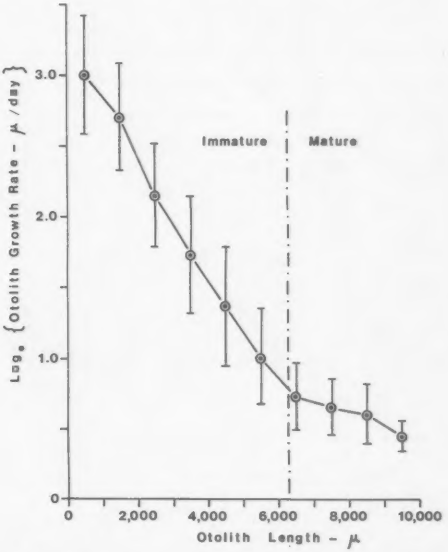

FIGURE 7.—Linearization of otolith growth rate data by logarithmic transformation for *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations.

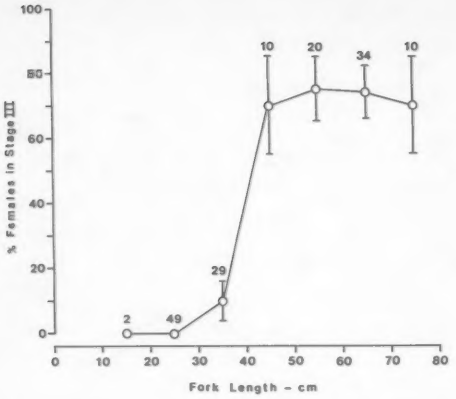

FIGURE 8.—Maturation in *Pristipomoides filamentosus* female. Stage III represents gravid/spawning individuals. Only samples collected during the spawning season are presented. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

growth rate, is completely counterintuitive to our understanding of the trade offs involved in optimizing growth and reproductive processes. Rather, it is more likely that episodic growth leaves an incomplete time record in the otolith (i.e., increments are not deposited) while concurrently, changes in otolith length are tightly coupled to changes in fork length (see Figure 5 where $r^2 = 0.899$). The resulting process would tend to underestimate Δt and thus to overestimate $\frac{d\ell}{dt}$. This hypothesis of interrupted otolith growth could explain the anomalous trend in otolith growth rates; consequently, we have regarded all data from otolith lengths >6,000 μm to be equivocal. We excluded these points from the remaining analyses, reducing the data set by 13% (2,957 ordered pairs to 2,577).

It is evident from Figure 7 that for otoliths ≤6,000 μm the logarithmic transformation was effective in linearizing the trend line and in stabilizing the variance, allowing the formulation of an analytical model describing the functional relationship between $\frac{d\ell}{dt}$ and ℓ. We write

$$\log_e \left(\frac{d\ell}{dt}\right) = \alpha - \beta\ell + \varepsilon \qquad (2)$$

where ℓ is otolith length in μm, t is time in days, α and β are model parameters, and ε is a normal random variable with mean zero and finite variance. When this model is cast in the form of Equation (1) and integrated, the solution is

$$\hat{T} = (e^{\alpha}\beta)^{-1}\,(e^{\beta L} - 1) \qquad (3)$$

where T is the estimate of age in days, and L is the total length of the otolith along the postrostral radial axis. Thus, to estimate the age of a sample specimen, one need only acquire estimates of α, β, and L.

Von Bertalanffy Growth Curve

A regression of log-transformed otolith growth rate against otolith length (Equation (2)) was performed for each of the 81 otolith samples. The age of each specimen was then estimated by Equation (3).

The fork length of the sample specimens is plotted against the point estimate of age in Figure 9. Because 13 of the 81 determinations were duplicates based on left and right otoliths from the same fish, and 4 of the remaining preparations had excessive coefficients of variation (≥20%), only 64 points are presented. These data were fitted to the von Bertalanffy growth model (Ricker 1979) using a nonlinear regression routine (NLIN Procedure) (Statistical Analysis System 1979). In this three-parameter formulation, L_∞ signifies the asymptotic upper bound on growth in length, K is an instantaneous growth-rate constant, and t_0 is a scaling factor equal to the X-intercept. When the model was freely fitted to the data, an unrealistically low estimate of L_∞ resulted (Table 2, solid line in Figure 9). As part of a related study in

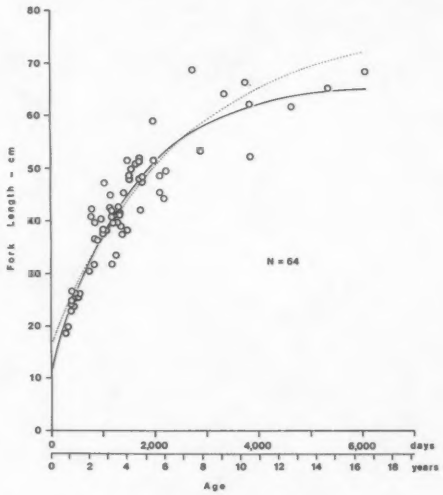

FIGURE 9.—Estimated growth curve for *Pristipomoides filamentosus*. Solid line represents a freely fitted von Bertalanffy curve whereas the L_∞ parameter was constrained to 78.0 cm in the fit of the dotted line.

TABLE 2.—Parameter estimates from the von Bertalanffy model fitted to 64 integrated age estimates of *Pristipomoides filamentosus*.

Parameter	Estimate	Standard error	Units
Freely fitted			
K	0.235	0.034	yr^{-1}
t_0	−0.807	0.298	yr
L_∞	66.4	28.15	cm
Constrained (L_∞ = 78.0 cm)			
K	0.146	0.010	yr^{-1}
t_0	−1.67	0.327	yr

which more than 2,500 opakapaka were measured, many fish exceeded 70 cm FL. Consequently, the 64 data points were refitted to the model with L_∞ constrained to a value of 78 cm FL, the largest specimen we have observed (Table 2, dotted line in Figure 9).

Analysis of Size-Frequency Distributions

The data presented in Figure 10 represent three length-frequency distributions of opakapaka sampled at French Frigate Shoals in the Hawaiian Islands. All three samples were taken on different dates but at the same position on the west side of the atoll (lat. 23°47'N, long. 166°22'W). In each distribution a large mode of small fish is plainly visible. If one accepts the premise that these small fish represent a single cohort of juveniles, these data afford the opportunity to estimate their size-specific growth rate by examining the progression of modes in time (Ricker 1975; McNew and Summerfelt 1978).

The simplified calculations presented in Table 3 show that these fish grew, on the average, at the rates of 0.020 cm/d during the winter growth period (October-May), 0.022 cm/d during the summer growth phase (May-November), and an average 0.021 cm/d over the entire year (October 1979-November 1980). If we compute the expected size-specific (31 cm FL) growth rate of these fish, based upon the fit of the integrated otolith age data to the von Bertalanffy model (Table 2, Fig. 9), we predict growth rates of 0.023 and 0.019 cm/d for the freely fitted and the constrained versions of the model, respectively. These results compare favorably with the modal growth rates, further substantiating our age estimates.

TABLE 3.—Growth rate calculations for *Pristipomoides filamentosus* based on size-frequency distributions. Samples from French Frigate Shoals, Hawaiian Islands.

	Sample no.		
	I	II	III
Date:	16 Oct. 1979	27 May 1980	3 Nov. 1980
Modal size (FL cm):	27.0	31.5	35.0
Samples compared	I-II	II-III	I-III
Elapsed time (d)	223	160	383
Change in length (cm)	4.5	3.5	8.0
Growth rate (cm/d)	0.020	0.022	0.021

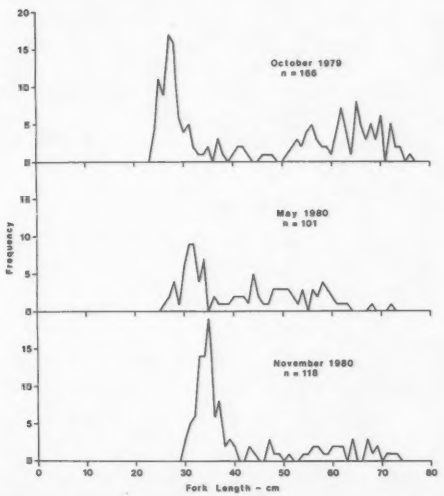

FIGURE 10.—Length-frequency distributions of *Pristipomoides filamentosus* sampled at French Frigate Shoals, Hawaiian Islands (lat. 23°47'N, long. 166°22'W).

DISCUSSION

Elsewhere we have shown that the increment thickness model presented here provides reasonably precise age estimates from a purely statistical standpoint (Ralston and Miyamoto 1981). The frequency distribution of coefficients of variation of T is centered on 6%, with 67 of the 81 values ≤10%. Thus, a typical preparation provides an age estimate for which the 95% confidence interval is about ±12% of the estimate. Furthermore, the regression technique is an effective means of accounting for variation in otolith growth rates. The frequency distribution of r^2 values for the 81 regressions had a median value of 78% (Ralston and Miyamoto 1981).

Several explicit and implicit assumptions, however, underlie the aging method presented here. It is important to address these at this time and to review to what extent they may or may not be justified. One important assumption is that it is appropriate to use the interpolative power of the regression Equation (2) to predict otolith growth rates in intermediate regions where increment microstructure is unclear. This

assumption implies that similar processes occur in regions of the otolith that appear somewhat different superficially. We feel it is not an unreasonable assumption, however, because one can usually enhance the quality of a preparation by increasing the amount of time and care devoted to it, bringing out distinct increments in regions which otherwise would remain uninterpretable. For example, Radtke (footnote 3) has shown that the core area of opakapaka otoliths requires substantially more etching time than does the marginal zone. He improved the quality of his samples by employing differential etching times, a tedious but effective technique. Wild and Foreman (1980) used similar methods in their study. Presumably, the visual quality of a preparation is largely limited by the ability of the investigator to unveil its contents.

A second and more important assumption is that it is reasonable to extrapolate the growth of a sexually mature fish based on its individual pattern of growth prior to gonad maturation. Because all data gathered at otolith lengths >6,000 μm were deleted, age estimates obtained from Equation (3) are bound by this constraint. We have argued that otolith increments become equivocal chronometers past maturity, due to interrupted growth. Both Pannella (1971) and Wild and Foreman (1980) reached similar conclusions in their studies of red hake, *Urophycis chuss*, and skipjack tuna, *Katsuwonus pelamis*, respectively. Significantly, in the latter study growth interruptions were not evident in yellowfin tuna, *Thunnus albacares*, and almost all specimens were of immature size (Schaefer et al. 1963). Not only has maturation been implicated in interrupting otolith growth, but also reduced food (Irie 1960; Methot and Kramer 1979; Uchiyama and Struhsaker 1981) and low temperature (Irie 1960; Taubert and Coble 1977). It is apparent from these studies that any factor which arrests the growth of the whole fish, temporarily or otherwise, can lead to errors in the time chronicle of daily increments (Pannella 1980). Clearly, if the additional energy burden incurred at sexual maturity is substantial (sensu Gadgil and Bossert 1970), extrapolation beyond 6,000 μm may be an unrealistic exercise and growth rates of large fish may in fact be overestimated. However, it is pertinent to note that the proportions in opakapaka of both ovarian and testicular tissues relative to total body weight are not great, ranging from 1 to 4% among Stage III females and slightly less among males (Ralston 1981). Furthermore, most models of fish growth currently in use (e.g., von Bertalanffy and Gompertz models) do not treat maturity as a growth singularity, i.e., a time when the pattern of growth changes. In spite of their relative simplicity, these models have adequately described fish growth dynamics in a surprisingly large number of situations (Ricker 1979). Undoubtedly this is because fine scale departures from model growth (e.g., seasonal trends) are averaged out when treating a lifespan measured in years. Finally, the procedure we have used involves extrapolating, at most, 68% beyond the range of the data (6,000-10,000 μm). In most cases, the amount we extrapolated was far less. Nonetheless, this particular assumption is critical and yet remains unresolved. Additional research on this topic is essential.

At the other extreme, by applying a linear model to the data (Equation (2)), we have assumed that otolith growth rate is greatest as otolith length approaches zero. This is unrealistic (see, for example, Pannella 1974; Brothers and McFarland 1981). The average width of increments actually decreases very near the focus (Fig. 2). We evaluated the extent of bias introduced by this computational simplification, however, by comparing age estimates derived from both analytical (Equation (3)) and complete numerical integration of all the otolith growth-rate data, broken down by 100 μm size classes. The largest absolute difference between the two types of age estimates was 18 d. This was for the youngest of fish, as might be expected, and indicates that the analytical method provides a poor approximation for fish <1 mo old. However, because our results are intended to describe growth over the entire size range of opakapaka, measured on a time scale of years, and because the difference between the two estimates becomes progressively smaller among the larger fish, we consider this a negligible error.

A final assumption is that one increment forms each day in preproductive individuals. We have presented evidence that validates this assumption, at least for fish 30-34 cm FL, in the form of in vivo marking of otoliths with tetracycline. Furthermore, evidence from the field (Fig. 10) also strongly supports this conclusion, again for immatures (27-35 cm FL). A final assessment of this assumption can be made by comparing the growth of opakapaka, as developed here, with studies available in the literature on lutjanid growth.

Researchers have long recognized the interdependence of growth parameters. Beverton and Holt (1959) presented values of K and L_∞ computed from the von Bertalanffy growth model and noted an inverse relationship between these parameters. Similarly, Cushing (1968) presented graphs relating growth parameters for several large taxonomic categories (e.g., Clupeoidei, Gadiformes, Salmonoidei, etc.). Pauly (1979) has attempted to quantify the relation-

ship between asymptotic weight (W_∞ or the weight of an individual at length L_∞) and K by developing the concept of the auximetric grid. He has argued that the logarithm of the product of K and W_∞ is relatively uniform for families of fishes. That is

$$P = \log_{10}(KW_\infty)$$

where P can be considered characteristic of taxa.

A review of the lutjanid growth literature allowed us to estimate P for lutjanids by computing the arithmetic average of the eight P values presented in Table 4 ($\bar{P} = 3.03$). An estimate of the asymptotic weight of opakapaka is 7,670 g (Ralston 1981). Using these two figures, we calculate an estimate of K for opakapaka to be 0.140 yr^{-1}. This figure compares very favorably with the estimate of K obtained from the constrained fit of the von Bertalanffy model to otolith data from immature fish presented earlier (0.146 yr^{-1}). The results of our marking experiments, length-frequency data, and literature comparisons all support the conclusion that increments are formed daily in subadult opakapaka (up to 3 yr old).

After considering all of the assumptions that underlie our analysis, we conclude that the results presented in Figure 9 accurately reflect the growth of opakapaka. Other investigators (Moffitt 1980; Radtke footnote 3) have presented growth curves for opakapaka, also based on otolith microstructure, but which show somewhat faster growth, especially for large, mature fish. Both studies were based upon complete counts of growth increments. We attribute the differences between our estimates and theirs to growth interruptions confounding the otolith time record in adults. These earlier studies neglected to entertain this possibility, an oversight which could lead to serious underestimates of age.

TABLE 4.—Growth relationships among the Lutjanidae with application of the auximetric grid (Pauly 1979).

Species	K (yr^{-1})	W_∞ (g)	P[1]	Source
Lutjanus apodus	0.180	3,774	2.83	Munro 1974
L. bohar	[2]0.106	9,100	2.99	Talbot 1960
L. campechanus	0.162	13,480	3.34	Nelson and Manooch 1982
L. johnii	[2]0.135	—	—	Druzhinin 1970
L. malabaricus	[2]0.064	13,600	2.94	Druzhinin 1970
L. purpureus	0.090	—	—	Menezes and Gesteira 1974
L. sanguineus	0.142	10,597	3.18	Lai and Liu 1974
	0.148	12,469	3.27	Lai and Liu 1974
L. synagris	[2]0.101	—	—	Druzhinin 1970
Ocyurus chrysurus	0.250	3,600	2.95	Munro 1974
Rhomboplites aurorubens	0.198	2,800	2.74	Grimes 1978

[1]$P = \log_{10}(KW_\infty)$.
[2]Estimated from Walford plots of size-at-age data.

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SPECIES ASSOCIATIONS AND DAY-NIGHT VARIABILITY OF TRAWL-CAUGHT FISHES FROM THE INSHORE SPONGE-CORAL HABITAT, SOUTH ATLANTIC BIGHT[1]

CHARLES A. WENNER[2]

ABSTRACT

Biomass, species composition, diversity, and community structure of demersal fishes were studied during the spring of 1978 in the sponge-coral habitat of the South Atlantic Bight. These results were compared with sampling at an open-shelf site. Otter trawl catch rates were an order of magnitude higher in the sponge-coral habitat than at the open-shelf site. Density and biomass estimates in the sponge-coral habitat averaged 384 individuals/ha and 31.0 kg/ha, respectively, whereas at the open-shelf site they averaged 57 individuals/ha and 3.2 kg/ha. In sponge-coral habitat samples, 101 species of demersal teleosts were taken. The Sparidae accounted for the greatest number of species (9), as well as 59% of the total number and 48% of the weight of demersal teleosts. Species diversity was highest in night-trawl tows in the sponge-coral habitat. Species associations, described by numerical classification, showed major differences in faunal assemblages between reef and open-shelf sites and between day and night samples.

Struhsaker (1969) presented a generalized habitat classification based on substrate type and species composition in a summary of demersal fish resources off the southeastern United States (Fig. 1). The open-shelf habitat extends offshore from 18 m (10 fm (fathoms)) to about 55 m (30 fm) and is characterized by a sandy bottom and relatively stable hydrographic conditions due to the moderating influence of the Gulf Stream (Struhsaker 1969; Mathews and Pashuk 1977). The ichthyofauna of the open shelf are relatively diverse but have a low biomass (Wenner et al. 1979a, b, c). Abundant teleostean families are the Sparidae, Synodontidae, Serranidae, Bothidae, and Triglidae (Wenner et al. 1979a).

The sponge-coral habitat (= Struhsaker's [1969] "live bottom") is composed of isolated areas within the open-shelf habitat. These locales have a hard substrate composed of a carbonate, shell, and quartz sand conglomerate which is either exposed or covered with a thin veneer of sand to a depth of 8 cm or less (Powles and Barans 1980). This substrate provides suitable sites for the growth of dense stands of attached invertebrates (sponges, corals, echinoderms, tunicates, hydroids, and bryozoans) and algae. A recent classification divides the sponge-coral habitat into estuarine and nearshore sites (<18 m [<10 fm]), intermediate sites (18-55 m [10-30 fm]), and offshore sites (55-183 m [30-100 fm]) (Miller and Richards 1979).

The most productive areas in the South Atlantic Bight, in terms of fish diversity and biomass, are the hard-bottom areas (Struhsaker 1969; Huntsman and Manooch 1978; Miller and Richards 1979; Powles and Barans 1980). The purposes of this report are to present distribution, relative abundance, and species composition of trawl-caught fishes from inshore and intermediate reefs sampled during the late spring of 1978 and to comment on the suitability of otter trawl gear for stock assessment of commercial finfish in this habitat.

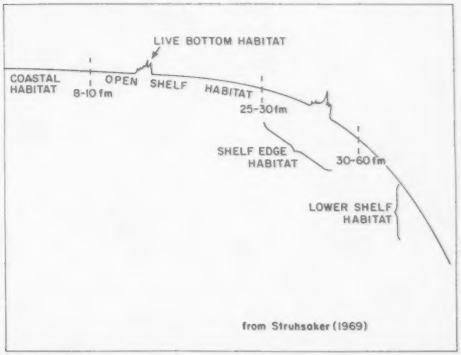

FIGURE 1.—South Atlantic Bight habitat types as defined by Struhsaker (1969).

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MATERIALS AND METHODS

Sampling was conducted at seven sites (Fig. 2) from 18 June to 16 July 1978 from the 32.6 m RV *Dolphin*. White line recorder tracings and bottom observations made with a Hydro Products TC-125 SDA[3] low light level underwater television system in conjunction with loran-C positions were used to produce maps of each site. The camera was suspended from the hydrographic wire (Fig. 3) and towed at low speed (~0.5 m/s; 1.0 kn) across each potential study area. The sponge-coral habitat was defined by the presence of attached invertebrate growth. In addition to the six sponge-coral habitat sites, an open-shelf (nonreef) area was studied to compare the species composition and biomass of both communities. Following habitat delineation, fishes were sampled by 10-min day and night trawl tows with a ¾ scale version of a Yankee No. 36 trawl (Wilk and Silverman 1976) at a speed of 6.5 km/h. The 16.5 m long footrope and the 11.9 m headrope of the net are attached to a 19 mm diameter ground cable by 12.7 mm diameter 11.6 m long leg lines. Each 17.7 m long ground cable attaches to a 226 kg wooden door. The footrope has about 1,000 rubber discs (114 mm diameter) attached to it which enable the net to bounce over small bottom irregularities. Day tows were made from 1 h after sunrise to 1 h before sunset, whereas night tows were made from 1 h after sunset to 1 h before sunrise.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

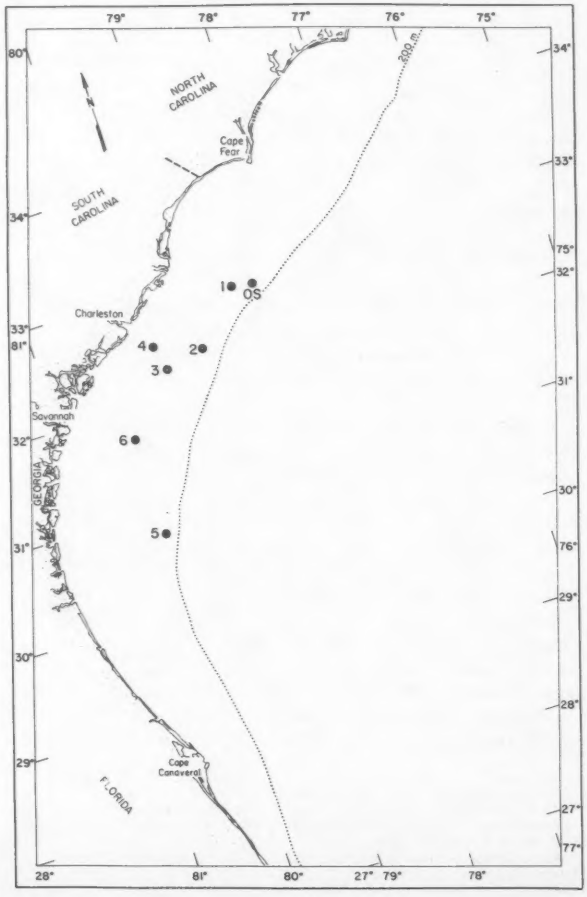

FIGURE 2.—Reef sampling sites for the 1978 survey. OS = open-shelf study area.

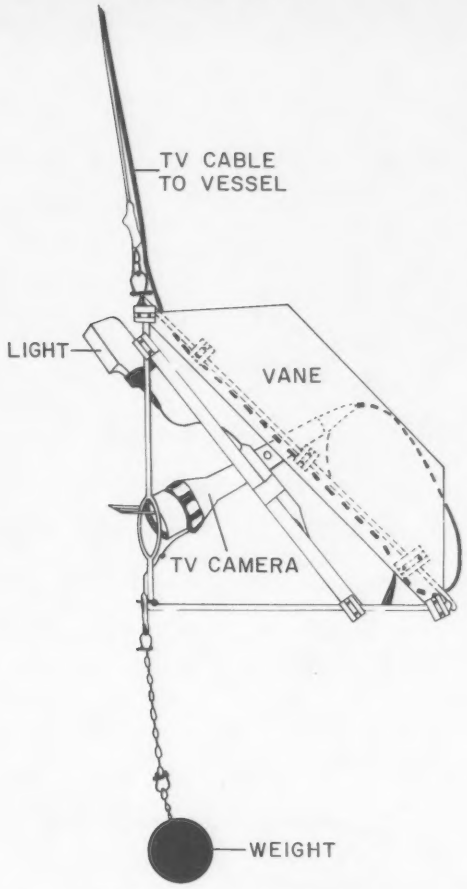

FIGURE 3.—System for deployment of underwater television equipment used in habitat documentation.

Fishes caught in nets that were not damaged during trawling operations were identified, measured, and weighed.

Initial calculations showed that the variance of the number of individuals per tow and the weight per tow far exceeded the mean and approximated a negative binomial distribution. Therefore, data were transformed ($\ln [x + 1]$) before analysis to standardize the variance and approximate the normal distribution (Taylor 1953; Elliott 1977). The number of species per tow was normally distributed and thus was not transformed. The Bliss (1967) approximation was used in retransforming the data from logarithmic to original units.

Since occasional catches of large elasmobranchs and large catches of pelagic fishes contributed significantly to the variance, biomass estimates were made only for demersal teleosts. Density estimates were calculated by the swept area method (Rohr and Gutherz 1977), with the sweep of the net being 8.748 m (Azarovitz[4]) and 1.080 km distances covered during a 10-min tow. These density estimates should be viewed as minimum, since the effectiveness of the ¾ Yankee trawl in sampling reef fish populations is unknown.

Species diversity (H') and its components, evenness (J') and richness, were calculated for elasmobranchs and demersal teleosts in each trawl tow using the following formulae:

$$H' = -\sum_{i=1}^{S} (p_i)(\log_2 p_i) \qquad \text{(Pielou 1969)}$$

where H' = index of species diversity expressed in bits/individual
S = number of species
p_i = proportion of total sample belonging to ith species;

$$J' = H'/H'_{\max} \qquad \text{(Pielou 1969)}$$

where J' = equitability or evenness
H' = observed species diversity
$H'_{\max} = \log_2 S$;

$$\text{Species richness} = S - 1/\ln N \qquad \text{(Margalef 1968)}$$

where S = number of species
N = number of individuals.

Normal and inverse cluster analysis (Clifford and Stephenson 1975) were used to analyze trawl data. Prior to the analysis, data were edited to eliminate species occurring in only one trawl tow. These species have no discernible distribution pattern and, therefore, contribute no information to the analysis (Boesch 1977). Species abundance scores were then $\log_{10}$ transformed, thus reducing the dominance of species having high abundance. The Bray-Curtis similarity coefficient (Clifford and Stephenson 1975) (= the Czekanowski Quantitative Index of Bloom 1981) was used on the modified data set and is expressed by

[4]T. Azarovitz, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun., 1977.

$$S_{jk} = 2\frac{\Sigma_i \min(X_{ij}, X_{ik})}{\Sigma_i (X_{ij} + X_{ik})}$$

where S_{jk} = similarity between entities j and k
X_{ij} = value of the ith attribute for entity j
X_{ik} = value of the ith attribute for entity k.

The Bray-Curtis similarity measure was chosen, since it most accurately reflects similarity in these types of analyses (Bloom 1981).

Normal analysis compared similarities among sites as indicated by the assemblages of fishes collected in trawl tows (entities are sites; attributes are the transformed species abundance scores). Inverse analysis compared similarities among the distribution patterns of species [entities are species, and attributes are the sites where they occur (Boesch 1977; Clifford and Stephenson 1975)]. The sorting strategy was flexible with $\beta = -0.25$ (see Clifford and Stephenson 1975 and Boesch 1977 for explanation).

Nodal analysis was used to examine the cooccurrence of species and site groups based on patterns of constancy and fidelity. Constancy, a measure of how consistently the members of a particular species group occur among the stations of a given site group, was calculated by the expression:

$$C_{ij} = a_{ij}/(n_i\, n_j) \qquad \text{(Boesch 1977)}$$

where C_{ij} = constancy of species group i in site group j
a_{ij} = actual number of individuals of species group i in site group j
$n_i n_j$ = number of entities in groups i and j, respectively.

Fidelity, the degree to which a given species group is restricted to a particular site group was determined by

$$F_{ij} = (a_{ij}\, \Sigma_j n_j / n_j\, \Sigma_j a_{ij}) \qquad \text{(Boesch 1977)}$$

where F_{ij} = fidelity of species group i in site group j
a_{ij} = actual number of individuals of species group i in collection group j
n_j = number of entities in group j.

RESULTS

Biomass

Otter trawl catches from the sponge-coral habitat were highly variable, ranging from 6 to 2,976 individuals (1.6-244.8 kg) in a standard tow (Table 1). The means of the natural log-transformed values of the number of individuals per haul from all reef sites were not significantly different between day and night ($t = 1.135$, df = 55), whereas mean weight of fishes was significantly greater in day tows ($t = 2.145$, df = 55). Mean values and density estimates for all trawl tows within the sponge-coral and open-shelf habitats were

	Mean values/tow		*Mean density estimates*[1]*/ha*	
Habitat	*No. individuals*	*Weight (kg)*	*No. individuals*	*Weight (kg)*
Sponge-coral	363	29.3	384	31.0
	[2](268; 491)	[2](24; 35.8)	[2](284; 520)	[2](25.4; 37.9)
Open shelf	54	3.0	57	3.2
	[2](24; 121)	[2](2.2; 4.0)	[2](25; 128)	[2](2.3; 4.2)

[1]Using 0.95 ha as the swept area of a standard tow.
[2]Upper and lower 90% confidence limits.

TABLE 1.—Mean catch/tow of demersal teleosts, 90% lower and upper confidence limits (LCL and UCL), and ranges for ¾ Yankee trawl tows by site for the spring 1978 sponge-coral survey, South Atlantic Bight.

Site	Depth (m)	Time	No. of tows	No. of individuals LCL	$\bar{x}$	UCL	Range	Weight (kg) LCL	$\bar{x}$	UCL	Range
Open shelf	46	Day	5	3	6	10	2-10	0.3	1.4	2.3	0.0-3.6
Open shelf	46	Night	6	55	75	101	42-101	3.1	4.4	6.2	1.9-6.2
Reef 1	37	Day	6	86	257	766	39-1,376	17.0	34.7	70.0	12.3-116.7
Reef 1	37	Night	5	105	172	280	64-248	12.9	16.7	21.7	11.2-24.0
Reef 2	44	Day	4	48	361	2,670	6-247	9.3	40.9	169.7	2.5-42.3
Reef 2	44	Night	4	103	164	260	87-214	13.7	19.1	26.5	11.7-25.6
Reef 3	29	Day	6	678	3,518	18,233	32-2,976	54.0	206.1	778.8	2.9-244.8
Reef 3	29	Night	6	125	188	284	66-307	14.1	19.8	27.6	8.1-27.8
Reef 4	18	Day	6	344	1,325	5,094	47-2,853	16.1	44.2	125.4	1.6-132.6
Reef 4	18	Night	7	148	220	328	64-413	8.5	13.8	23.0	2.6-27.6
Reef 5	42	Day	4	198	599	1,812	108-847	14.7	23.9	35.7	14.6-37.3
Reef 5	42	Night	1	—	45	—	—	—	12.0	—	—
Reef 6	27	Day	2	—	100	—	79-118	—	13.9	—	13.0-14.7
Reef 6	27	Night	6	110	150	205	86-202	13.1	18.1	24.9	10.9-32.3

Species Composition and Relative Abundance

Eleven trawl tows in the open-shelf habitat collected 470 individuals distributed among 26 species (16 families) with a total weight of 31.4 kg. Day catches (11 species, 8 families) accounted for only 6% of the number and 18% of the total weight of demersal teleosts taken at this site, and were not dominated by a single species. Night tows (22 species, 13 families) were dominated by planehead filefish, *Stephanolepis hispidus*, which accounted for 68% of the number and 46% of the weight of demersal teleosts at the open-shelf site (Table 2).

Trawl tows in the sponge-coral habitat ($n = 57$) collected 22,046 demersal teleosts belonging to 102 species (37 families) and having a total weight of 1,832 kg (Table 3). The Sparidae dominated the catches with the greatest number of species (9) and accounted for 59% of the total number and 48% of the total weight of demersal teleosts. The five most numerically abundant families comprised 92% and 77% of the total catch by numbers and weight. The 10 most numerically abundant species accounted for 54% of the total abundance in all 57 trawl tows. Catches of the southern porgy, *Stenotomus aculeatus*, were an order of magnitude higher than those of other species (Table 4), contributing 57.3% of the total. This species also ranked first by weight, comprising 42.1% of the trawl-caught fish weight (Table 5).

Community Structure

One's perception of fish community structure in the South Atlantic Bight depends upon the habitat and time of sampling. Numerical classification indicated that four major divisions were present, consisting of 12 site groups (Fig. 4). The first major division contained, with one exception, otter trawl collections made during the day (site group 1) and night (site group 2) in the open-shelf area. A second division within the classificatory scheme included all trawl tows from reef 5 (site group 3). The two remaining broad divisions were composed of day tows (site groups 4 through 7) and night tows (site groups 8 through 12) from the five remaining reef sites. In general, major faunal distinctions were made, not only between collections from different habitats (open shelf vs. reef), but also between day and night samples taken at the same site.

The groundfish communities of the open-shelf and sponge-coral habitat formed 9 species groups containing from 5 to 11 species (Fig. 5). Each group was associated with specific spatial and temporal conditions. The five species of demersal fishes in group A showed a high frequency of occurrence and abundance at all reef sites, as reflected in the moderate to very high nodal constancy values (Fig. 6). The low and moderate constancy values for this species group in site groups 1 (5 open-shelf day tows, 1 day tow at reef 2) and 2 (6 open-shelf night tows) are a result of

TABLE 2.—Demersal teleosts taken in ¾ Yankee trawl tows at the open-shelf study site, South Atlantic Bight, spring 1978. n = number of occurrences in 5 day or 6 night otter trawl tows.

		Day			Night		
			weight			weight	
Family	Species	No.	(kg)	*n*	No.	(kg)	*n*
Muraenidae	*Gymnothorax saxicola*	—	—	—	4	0.37	3
Synodontidae	*Synodus foetens*	3	0.57	2	—	—	—
	Synodus intermedius	2	0.14	2	3	0.40	1
	Trachinocephalus myops	—	—	—	1	0.08	1
Ogcocephalidae	*Ogcocephalus parvus*	2	0.04	1	1	0.01	1
Ophidiidae	*Ophidion beani*	—	—	—	4	0.23	3
	Ophidion holbrooki	—	—	—	4	0.34	2
Serranidae	*Centropristis ocyurus*	3	0.09	1	17	1.02	6
	Diplectrum formosum	3	0.23	2	9	1.13	3
Priacanthidae	*Pristigenys alta*	—	—	—	1	0.03	1
Lutjanidae	*Rhomboplites aurorubens*	—	—	—	2	0.10	2
Haemulidae	*Haemulon aurolineatum*	—	—	—	69	6.20	3
Sciaenidae	*Equetus lanceolatus*	—	—	—	2	0.09	1
Mullidae	*Mullus auratus*	—	—	—	1	0.07	1
Labridae	*Hemipteronotus novacula*	2	0.13	1	—	—	—
Scorpaenidae	*Scorpaena brasiliensis*	—	—	—	1	0.19	1
Dactylopteridae	*Dactylopterus volitans*	2	2.3	1	—	—	—
Bothidae	*Bothus ocellatus*	—	—	—	1	0.02	1
	Cyclopsetta fimbriata	—	—	—	1	0.09	1
	Gastropsetta frontalis	—	—	—	2	0.11	2
	Paralichthys dentatus	—	—	—	1	0.40	1
	Syacium papillosum	1	0.30	1	2	0.37	2
Balistidae	*Aluterus heudeloti*	2	1.60	1	1	0.05	1
	Monacanthus ciliatus	—	—	—	1	0.03	1
	Stephanolepis hispidus	4	0.14	3	315	14.30	6
Tetraodontidae	*Sphoeroides dorsalis*	3	0.19	3	—	—	—

TABLE 3.—Families and species of demersal fishes taken in 57 ¾ Yankee trawl tows in the sponge-coral habitat, South Atlantic Bight, during the spring of 1978. * = <0.1 kg.

Family	Species	No.	Weight (kg)	Family	Species	No.	Weight (kg)
Carcharhinidae	*Rhizoprionodon terraenovae*	1	1.3	Sciaenidae	*Equetus lanceolatus*	72	8.1
Rajidae	*Raja eglanteria*	11	6.6		*Pareques acuminatus*	1	*
Dasyatidae	*Dasyatis americana*	2	3.0		*Pareques umbrosus*	178	12.6
	Dasyatis centroura	1	90.7	Mullidae	*Mullus auratus*	12	0.6
	Dasyatis sayi	1	0.1	Chaetodontidae	*Chaetodon aya*	4	0.3
Muraenidae	*Anarchias yoshiae*	3	*		*Chaetodon ocellatus*	33	7.5
	Gymnothorax moringa	1	0.1		*Chaetodon sedentarius*	21	1.2
	Gymnothorax saxicola	6	0.9		*Chaetodon striatus*	1	0.1
	Muraena retifera	1	0.1	Pomacanthidae	*Holacanthus isabelita*	263	167.9
Congridae	*Ariosoma balearicum*	1	*		*Holacanthus ciliaris*	2	1.0
	Conger oceanicus	4	0.2		*Pomacanthus paru*	2	0.2
Synodontidae	*Saurida brasiliensis*	1	*	Pomacentridae	*Chromis enchrysurus*	1,801	40.0
	Synodus foetens	19	2.5	Labridae	*Halichoeres bathyphilus*	1	0.1
	Synodus intermedius	17	1.5		*Halichoeres bivittatus*	8	0.4
	Synodus poeyi	24	0.1		*Halichoeres caudalis*	10	0.4
	Trachinocephalus myops	2	0.2		*Hemipteronotus novacula*	2	0.2
Batrachoididae	*Opsanus* c.f. *pardus*	7	0.1	Labridae unidentified		1	*
	Porichthys plectrodon	44	0.9	Scaridae	*Nicholsina usta*	1	*
Gobiesocidae	*Gobiesox strumosus*	1	*	Uranoscopidae	*Kathetostoma albigutta*	11	0.5
Antennariidae	*Antennarius ocellatus*	1	0.5	Clinidae	*Starksia ocellata*	8	*
Ogcocephalidae	*Halieutichthys aculeatus*	1	*	Blenniidae	*Hypleurochilus geminatus*	4	*
	Ogcocephalus corniger	2	0.2		*Parablennius marmoreus*	32	*
Gadidae	*Urophycis earlii*	19	3.0	Callionymidae	*Callionymus pauciradiatus*	1	*
	Urophycis regia	5	0.3	Gobiidae	*Evermanichthys spongicola*	1	*
Ophidiidae	*Ophidion beani*	11	0.7		*Ioglossus calliurus*	1	*
	Ophidion holbrooki	51	4.0	Scorpaenidae	*Scorpaena brasiliensis*	17	2.7
	Ophidion selenops	6	*		*Scorpaena calcarata*	16	0.7
	Otophidium osmostigmum	4	*		*Scorpaena dispar*	2	0.2
Carapidae	*Carapus bermudensis*	22	0.1		*Scorpaenodes tredecimspinosus*	1	*
Holocentridae	*Holocentrus ascensionis*	2	0.6	Triglidae	*Prionotus carolinus*	120	7.5
Syngnathidae	*Hippocampus erectus*	3	0.1		*Prionotus ophryas*	9	0.7
Serranidae	*Centropristis ocyurus*	158	6.9		*Prionotus roseus*	5	0.3
	Centropristis striata	435	61.6		*Prionotus salmonicolor*	1	0.2
	Diplectrum formosum	84	5.0		*Prionotus scitulus*	7	0.3
	Mycteroperca microlepis	5	24.2	Bothidae	*Ancylopsetta quadrocellata*	18	6.2
	Mycteroperca venenosa	1	0.1		*Bothus ocellatus*	11	0.4
	Serranus phoebe	37	5.0		*Bothus robinsi*	7	0.2
Priacanthidae	*Priacanthus arenatus*	5	1.9		*Cyclopsetta fimbriata*	5	0.5
	Pristigenys alta	31	4.7		*Etropus microstomus*	3	*
Apogonidae	*Apogon pseudomaculatus*	174	0.4		*Paralichthys albigutta*	2	1.0
Lutjanidae	*Lutjanus campechanus*	3	0.4		*Paralichthys dentatus*	19	5.4
	Rhomboplites aurorubens	384	33.7		*Paralichthys lethostigma*	1	0.6
Haemulidae	*Haemulon aurolineatum*	3,153	239.5		*Syacium papillosum*	24	2.7
	Haemulon plumieri	16	13.6	Balistidae	*Aluterus heudeloti*	7	3.3
	Orthopristis chrysoptera	1	0.2		*Aluterus schoepfi*	28	19.8
Sparidae	*Archosargus probatocephalus*	11	11.7		*Balistes capriscus*	20	25.7
	Calamus bajonado	2	9.3		*Monacanthus ciliatus*	3	0.1
	Calamus leucosteus	319	135.4		*Stephanolepis hispidus*	1,392	93.8
	Calamus nodosus	25	26.6	Ostraciidae	*Acanthostracion polygonius*	2	1.4
	Diplodus holbrooki	3	0.2		*Acanthostracion quadricornis*	53	21.5
	Lagodon rhomboides	2	0.2	Tetraodontidae	*Spoeroides spengleri*	6	0.4
	Pagrus pagrus	46	23.5	Diodontidae	*Chilomycterus schoepfi*	8	2.9
	Stenotomus aculeatus	12,630	771.2		*Diodon holacanthus*	4	1.0
	Stenotomus caprinus	1	*				

the infrequent occurrence of *Stephanolepis hispidus* and *Haemulon aurolineatum* in some of these tows. The widespread distribution pattern of this species group is apparent in the low nodal fidelity values (Fig. 7).

Species group B consisted of an assemblage of fishes that were widely distributed in night reef samples. Species showed very low to low constancy and negative fidelity to site groups 1 through 7. Group B species displayed moderate to high constancy in the remaining site groups which consisted entirely of night trawl tows. This wide distributional pattern among night samples was reflected in the low fidelity values for all site groups.

Fishes of group C, although not very abundant, occurred almost exclusively in night trawl tows. Species in this group had low and high constancy, moderate and high fidelity to site groups 8 and 9, respectively, which were composed of night trawl tows from reefs 1 (38 m) and 2 (44 m). *Synodus intermedius* was the only species of this group that had a wide distribution in other site groups regardless of time of collection. *Bothus robinsi* and *Prionotus roseus* were found only in site groups 8 and 9, whereas the remaining species (*Kathetostoma albigutta*, *Cyclopsetta fimbriata*, *Ophidion selenops*, *Otophidium omostigmum*) occurred only in night tows of these and other site groups.

TABLE 4.—Ten most numerically abundant demersal teleosts taken spring 1978 in 57 sponge-coral habitat trawl tows, South Atlantic Bight.

Species	No. of individuals	% of total catch	Cumulative %	No. of occurrences
Stenotomus aculeatus	12,630	57.3		40
Haemulon aurolineatum	3,153	14.3	71.6	49
Chromis enchrysurus	1,801	8.2	79.8	9
Stephanolepis hispidus	1,392	6.3	86.1	52
Centropristis striata	435	2.0	88.1	37
Rhomboplites aurorubens	384	1.7	89.8	20
Calamus leucosteus	319	1.4	91.2	44
Holacanthus isabelita	263	1.2	92.4	28
Pareques umbrosus	178	0.8	93.2	24
Apogon pseudomaculatus	174	0.8	94.0	16

TABLE 5.—Ten most important demersal teleosts by weight in 57 sponge-coral habitat trawl tows taken spring 1978, South Atlantic Bight.

Species	Weight (kg)	% of catch	Cumulative %	No. of occurrences
Stenotomus aculeatus	771.2	42.1		40
Haemulon aurolineatum	239.5	13.1	55.2	49
Holacanthus isabelita	167.9	9.2	64.4	28
Calamus leucosteus	135.4	7.4	71.8	44
Stephanolepis hispidus	93.8	5.1	76.9	52
Centropristis striata	61.6	3.4	80.3	37
Chromis enchrysurus	40.0	2.2	82.5	9
Rhomboplites aurorubens	33.7	1.8	84.3	20
Calamus nodosus	26.6	1.4	85.7	11
Balistes capriscus	25.7	1.4	87.1	7

The five species of group D were rare in the trawl collections but had their greatest frequency of occurrence in night trawl tows from reef sites in depths >30 m. Members of group E were more abundant than group D and were collected primarily in night samples. They were not, however, restricted to reef sites, since five species (*Synodus foetens*, *Aluterus heudeloti*, *Scorpaena brasiliensis*, *Syacium papillosum*, and *Ophidion beani*) cooccurred in site group 2 (night open-shelf collections). Generally, this group was rarely found in day trawl tows but was widely distributed and abundant in night samples from all sites.

Species group F occurred almost exclusively at night and was most frequently encountered and abundant at site group 10 (6 night tows at reef 3; 1 night tow at reef 4). Low constancy values were observed for species at site groups 2, 7, 8, 9, and 12, whereas they exhibited high constancy and fidelity values for site group 10.

Group G had seven species that were relatively rare but most frequently found in daytime tows with maximum abundances in site group 7 (11 day samples from 4 reef areas). Group H also contained fishes that were widely distributed among site groups but not very abundant. Highest constancy and fidelity values were in site group 3 where species in group H had maximum abundance and frequency of occurrence.

Although members of species group I were found in several site groups, this assemblage was considered to be a regular component of the deeper reef sites where their greatest frequencies of occurrence and abundance were observed in day tows. Their affinity for deeper reefs is supported by high constancy and fidelity values in site groups 4 (3 day tows at reef 2, depth = 44 m), and moderate constancy and fidelity values in site groups 3 (4 day and 1 night tow at reef 5, depth = 42 m) and 5 (5 day tows at reef 1, depth = 37 m).

Diversity

More species were collected in night trawl tows in both open-shelf and reef habitats than in day tows. Comparisons of the mean number of species per tow in day and night samples at the open-shelf site showed night tows ($\bar{x} = 7.3$) had significantly more species than day tows ($\bar{x} = 3.6$) at the 95% probability level ($t = 2.905$, df = 9). The same trend was observed for samples from the sponge-coral habitat, pooled by time of collection. The 28 day tows had significantly fewer species ($\bar{x} = 10.8$) than night tows ($\bar{x} = 19.6$) at the 99% level ($t = 7.777$, df = 55).

Comparisons of the number of species per tow for each time period in the two habitat types showed that mean values for the open-shelf habitat were one-third to one-half the mean values for various reef sites. Night tows in the reef habitat had higher species diversity values than day tows. This was attributed to increased evenness and species richness (Table 6).

DISCUSSION

Standard otter trawl collections in the sponge-coral habitat (inshore and intermediate reefs of Miller and Richards 1979) yielded demersal teleost biomass estimates that were an order of magnitude higher than those of the open shelf (Table 7). Although these

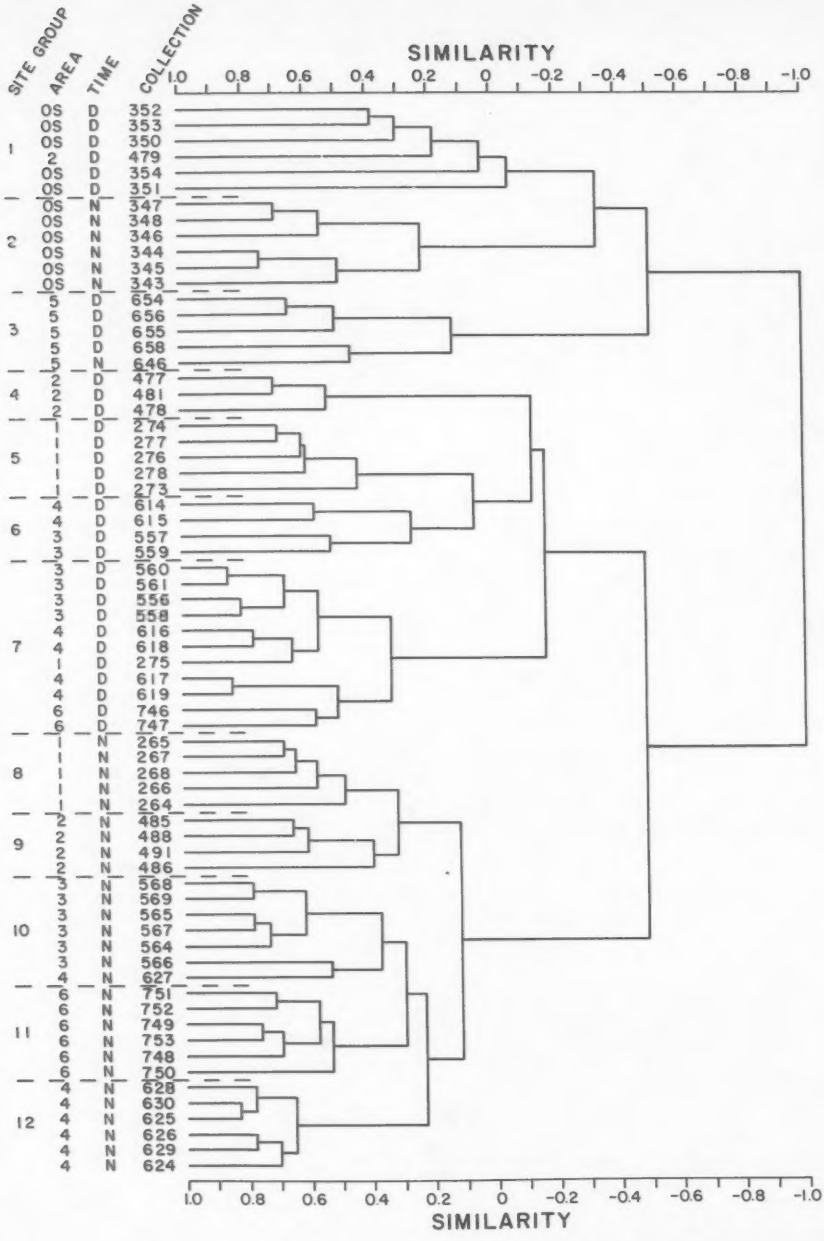

FIGURE 4.—Normal analysis (station cluster) of 1978 late spring sponge-coral habitat survey. OS = open shelf; D = day; N = night. Area refers to collection location; see Figure 2.

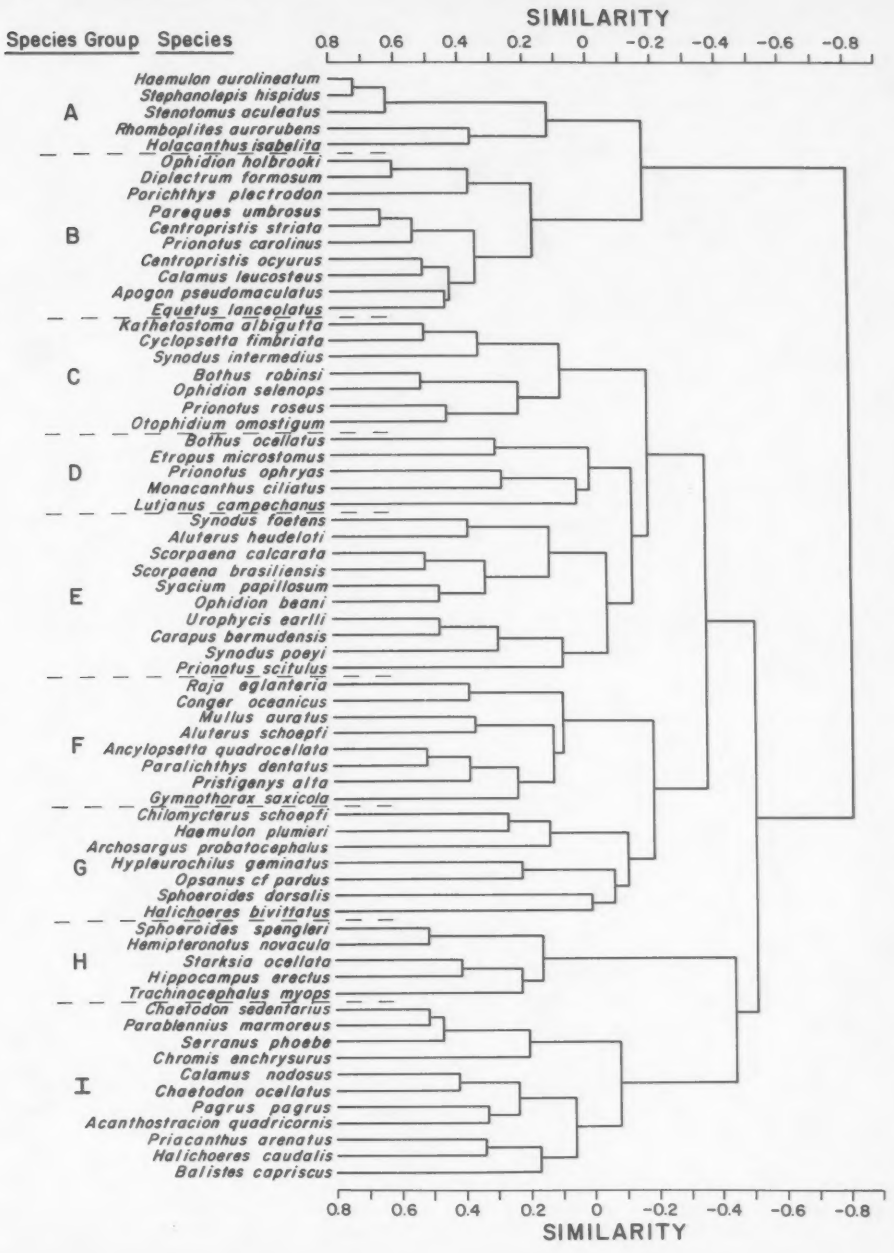

FIGURE 5.—Inverse analysis (species cluster) of 1978 late spring sponge-coral habitat survey.

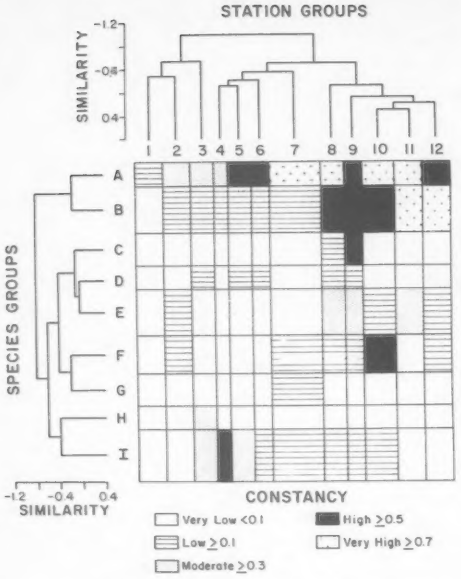

FIGURE 6.—Nodal constancy for station and species groups as defined by cluster analysis for the 1978 late spring sponge-coral habitat survey.

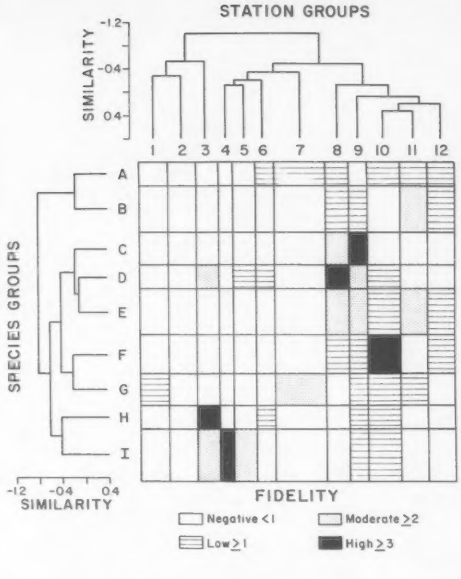

FIGURE 7.—Nodal fidelity for station and species groups as defined by cluster analysis for the 1978 late spring sponge-coral habitat survey.

TABLE 6.—Number of species/tow, diversity, evenness and species richness values for demersal fishes taken spring 1978 in ¾ Yankee trawl tows in the open shelf and sponge-coral habitat, South Atlantic Bight, LCL and UCL = lower and upper 90% confidence limits.

Site	Time	No. of species LCL	$\bar{x}$	UCL	Range	Diversity (bits/individuals) range	Evenness range	Species richness range
Open shelf	Day	1.9	3.6	5.3	2-7	0.918-2.646	0.918-1.000	0-1.242
Open shelf	Night	5.5	7.3	9.1	4-10	0.443-1.947	0.221-0.586	0.779-2.140
Reef 1	Day	9.0	13.3	17.6	6-22	1.697-3.185	0.380-0.920	1.364-3.143
Reef 1	Night	17.2	20.0	22.8	16-24	2.102-3.667	0.525-0.863	2.867-4.312
Reef 2	Day	3.8	9.2	14.7	5-15	0.383-2.251	0.148-0.394	0.911-2.541
Reef 2	Night	17.4	23.8	30.2	16-28	3.108-3.408	0.677-0.819	3.350-5.175
Reef 3	Day	7.0	9.2	11.4	6-13	0.311-2.119	0.093-0.706	0.894-1.849
Reef 3	Night	18.1	21.8	25.7	16-27	1.494-3.727	0.373-0.817	2.619-4.990
Reef 4	Day	9.1	10.0	10.9	9-12	0.621-2.621	0.196-0.789	1.131-2.324
Reef 4	Night	12.5	15.4	18.3	9-21	2.227-3.171	0.559-0.746	1.923-3.336
Reef 5	Day	6.9	12.5	18.1	8-18	0.131-1.037	0.041-0.345	1.212
Reef 5	Night	—	18.0	—	—	3.758	0.901	4.465
Reef 6	Day	—	10.5	—	8-13	1.654-2.515	0.551-0.697	1.467-2.746
Reef 6	Night	16.9	19.5	22.1	15-22	3.063-3.575	0.714-0.827	3.065-4.265

compared closely with values for a reef at a depth of 37 m off the South Carolina coast (Powles and Barans 1980), they were one to two orders of magnitude lower than tropical reef systems (Table 7), with the exception of an estimate of 40.4 kg/ha based on five visual transects at Rabbit Island in Hawaii (Brock 1954). This latter value, however, was indicative of marginal reef habitat, since the estimate was derived from counts taken largely over sandy bottom with an occasional rocky ledge or coral head.

Edwards (1968) provided a rationale for obtaining biomass estimates from otter trawl catches for resource surveys in the western North Atlantic. Catches are adjusted on a species-by-species basis using a correction factor which is derived from the individual species' availability and vulnerability to the survey gear. In addition, areal and seasonal changes in the species' distribution pattern are figured into the adjustment. Correction factors are determined from long-term distribution and relative

TABLE 7.—Summary of biomass estimates from South Atlantic Bight sponge-coral and open-shelf habitats and selected tropical reefs.

Area	kg/ha	Citation	Comments
South Atlantic Bight sponge-coral	27.3	Powles and Barans 1980	
South Atlantic Bight sponge-coral	31.0	Present study	
South Atlantic Bight open-shelf	5.6	Wenner et al. 1979a	fall, 1973
South Atlantic Bight open-shelf	5.0	Wenner et al. 1979b	spring, 1974
South Atlantic Bight open-shelf	2.9	Wenner et al. 1979c	summer, 1974
South Atlantic Bight open-shelf	3.2	Wenner et al. 1979d	winter-early spring, 1975
South Atlantic Bight open-shelf	3.2	Present study	
Keahole Point, Hawaii	1,856	Brock 1954	rock, boulders and coral
Waiane, Hawaii	417	Brock 1954	rock, coral and small sand patches
Hilo, Hawaii	214	Brock 1954	rock and coral
Waikiki, Hawaii	195	Brock 1954	some rock and coral, mostly thin sand over rock
Kealekekua Bay, Hawaii	145	Brock 1954	rock and coral with sand
Kumakahi Puna, Hawaii	144	Brock 1954	rock and sand, little coral
Hanauma Bay, Hawaii	154	Brock 1954	sand, rock and coral
Rabbit Island, Hawaii	40	Brock 1954	largely sand; occasional rocky ledge or coral head
Bermuda	490	Bardach 1959	
Virgin Islands	1,600	Randall 1963	

abundance data, observations from submersibles, underwater television observations of fish and their reactions to trawls, and comparative gear observations. Since we lack the necessary data to compile these values for South Atlantic Bight reef species and, hence, to judge trawl efficiency in sampling this habitat, the estimates of the present study should be considered minimum values. However, some qualitative gear efficiency observations can be made.

Since the ¾ Yankee otter trawl net has an average vertical mouth opening of only 1.25 m at a towing speed of 6.5 km/h, it is inefficient in sampling many of the commercially important lutjanids and sparids. Although *Pagrus pagrus*, the most commercially important sparid in the South Atlantic Bight (Ulrich et al. 1976), is a generalized benthic feeder (Manooch 1977), it frequently forms aggregations 2 m off the bottom on intermediate depth reefs. Vermilion, *Rhomboplites aurorubens*, and red snapper, *Lutjanus campechanus*, often show the same behavior. Although these species are represented in trap collections from various reef sites and are taken with hook-and-line gear, their low relative abundance (with the exception of small *R. aurorubens* in day trawl tows) can be explained by their unavailability to the net due to their position in the water column.

Comparisons of the dominant species from sponge-coral and open-shelf habitat studies in the South Atlantic Bight show that, with one exception, the sparid *Stenotomus aculeatus* is the most numerous trawl-caught demersal teleost. Powles and Barans (1980) cited tomtate, *Haemulon aurolineatum*, as the most abundant fish taken with the ¾ Yankee trawl at a sponge-coral site at a depth of 37 m. *Stenotomus aculeatus* taken in stratified-random otter trawl sampling in the open-shelf habitat were most abundant in depths <28 m (Wenner et al. 1979a, b, c, d). The means of the natural logarithmic values of the number of *S. aculeatus* per tow for each of the sponge-coral habitat sites are negatively correlated with the depth of the site ($r = -0.89$, $n = 7$). The numerical dominance of tomtate in the previous trawl study (Powles and Barans 1980) is a reflection of the greater site depth.

The most apparent feature of the species diversity and community analysis is the marked difference between day and night tows. The increased species diversity for night collections is attributed to a greater number of species and a more even distribution of individuals among species. Hoese et al. (1968) reported more species taken in night than day trawl tows in Texas coastal waters and attributed the differences to changes in species availability (movement from the sampling area; vertical movement above the headrope; burrowing into the substrate) or vulnerability (increased daytime net avoidance due to trawl visibility).

Most reef studies using visual census techniques have shown the diversity of fish species to be higher during the day than at night (Collette and Talbot 1972; Goldman and Talbot 1976; Helfman 1978). The results of the present study indicate the opposite to be true. Day trawl tows in the sponge-coral habitat had a lower diversity because these areas lack many of the diurnal species of labrids, scarids, pomacentrids, and acanthurids found in tropical systems. In addition, where night trawl samples contained fish that may be diurnal, the lack of hiding places associated with the luxuriant coral growth in the tropics increased the vulnerability of these fish to night trawl tows, despite the fact they were not actively moving about and feeding.

In the present study, certain families were collected more frequently in, or were restricted to, night trawl tows (Table 8). Ophidiids (4 species), sciaenids (3 species), and gadids (2 species) occurred only in night tows. Seven of the 15 most abundant species were taken significantly more frequently in night collections (Table 9). The explanation for these patterns varies according to the species.

The significantly greater frequency of occurrence in night catches of black sea bass, *Centropristis striata*, was caused by this species' increased vulnerability to night trawl tows. Trap and handline collections, as well as underwater television observations, have shown *C. striata* to be much more abundant than was indicated by our otter trawl tows. This supports the findings of Powles and Barans (1980).

Ophidioid fishes of the sponge-coral habitat are nocturnal species that were unavailable to day trawl tows. Starck and Davis (1966) indicated that although cusk eels were abundant in rotenone collections, they were never visually observed moving about reef systems during the day. These investigators found, however, that *Ophidion holbrooki* was active over the sandy portion of a Florida reef at night. When this species was disturbed with lights, it burrowed tail-first into the sand. Another species (*O. selenops*) was seen by Starck and Davis (1966) swimming near bottom in night dives at deeper water reef sites. The four species (*O. holbrooki*, *O. beani*, *O. selenops*, *Otophidium omostigmum*) collected during the present study were taken only in night trawl tows indicating that because of their daytime burrowing behavior, cusk eels are unavailable to day collections.

Atlantic midshipman, *Porichthys plectrodon*, is another nocturnal species that burrows into the sediment during daylight thus making itself unavailable to day trawl tows (Lane 1967). In laboratory tests (Lane 1967), *P. plectrodon* emerged from the substrate 45 min after sunset and burrowed about 45 min to 1 h before sunrise. Nocturnal feeding on near-bottom crustacean plankton was shown (Lane 1967).

Sciaenids (*Pareques umbrosus*, *Equetus lanceolatus*, *P. acuminatus*) were absent from all day samples but occurred in 27 of 29 night tows. Their absence from day collections can more likely be attributed to their unavailability rather than their decreased vulnerability to day trawl tows. Unlike the burrowing ophidioids and *Porichthys plectrodon*, these secretive sciaenids (Parker et al. 1979) seem to hide around or under available structures. Starck and Davis (1966) reported that *Pareques acuminatus* hides under rocks on the reef during the day and ventures out to feed at night. Hobson (1965) indicated that the closely related *P. viola* is a nocturnal foraging fish that hides under ledges and rocks during the day.

The daytime residence of *Apogon pseudomaculatus* in caves and crevices on the reef (Starck and Davis 1966) effectively excluded this species from the sampling capability of the trawl. The emergence of *A. pseudomaculatus* and other apogonids at night to forage on midwater plankton over the reef (Collette and Talbot 1972) explains the occurrence of this species only in night tows.

Triglids (*Prionotus carolinus*, *P. ophryas*, *P. scitulus*, *P. roseus*, *P. salmonicolor*) were found in only a single day tow but were in 23 of 29 night tows. The dominant northern searobin, *P. carolinus*, is a nocturnal species, however, which would seem to suggest that its greater frequency of occurrence in night trawl tows cannot readily be explained by a concomitant increase in its vulnerability to the gear. *Prionotus carolinus* is a common member of the South Atlantic Bight open-shelf ichthyofauna in depths from 9 to 55 m (Wenner et al. 1979a). Analysis of stratified, random ¾ Yankee trawl collections from summer 1974 and 1975 and fall 1973 showed that although this

TABLE 8.—Families of fishes taken primarily in night otter trawl tows in the sponge-coral habitat of the South Atlantic Bight.

Family	Day		Night	
	Present	Absent	Present	Absent
Ophidiidae	0	28	24	5
Scorpaenidae	2	26	16	13
Triglidae	1	27	23	6
Synodontidae	4	24	17	12
Bothidae	5	23	26	3
Sciaenidae	0	28	27	2
Gadidae	0	28	13	16
Batrachoididae	1	27	12	17

TABLE 9.—Comparison of frequency of occurrence of the 15 most numerically abundant species in day and night trawl tows in the sponge-coral habitat, South Atlantic Bight. * = significant at the 95% probability level.

Species	Day tows		Night tows		χ^2
	Present	Absent	Present	Absent	
Stenotomus aculeatus	17	11	23	6	1.54
Haemulon aurolineatum	20	8	28	1	5.00*
Chromis enchrysurus	7	21	2	27	0.07
Stephanolepis hispidus	23	5	28	1	1.79
Centropristis striata	13	15	24	5	6.73*
Rhomboplites aurorubens	12	16	6	23	2.29
Calamus leucosteus	22	6	22	7	0.01
Holacanthus isabelita	17	11	11	18	1.38
Pareques umbrosus	0	28	11	18	10.83*
Apogon pseudomaculatus	0	28	16	13	18.83*
Prionotus carolinus	0	28	17	12	20.67*
Acanthostracion quadricornis	13	15	13	16	0.00
Ophidion holbrooki	0	28	22	7	31.46*
Porichthys plectrodon	0	28	11	18	10.83*
Chaetodon ocellatus	8	20	6	23	0.07

species was encountered in more night (53%) than day tows (12%), the frequency of occurrence was not significantly different ($x^2 = 0.18$, df = 108). Based on the percent of fish with stomach contents, Ross (1977) found that peak feeding activity for eight species of searobins (*P. carolinus* not included) was in the morning. He indicated, however, that these triglids had some food items in the stomach at all times. Bigelow and Schroeder (1953) noted that *P. carolinus* burrows with only the eyes and head showing, and Bardach and Case (1965) confirmed that this species buries itself in the substrate. The available evidence, then, indicates that *P. carolinus* is a nocturnally active species that either buries itself in the sandy portions of the sponge-coral habitat during the day or makes nocturnal feeding forays into this habitat from the surrounding sandy areas where it resides during the day. Conclusive evidence can only be obtained from analysis of its food habits as determined from specimens collected in the sponge-coral habitat.

Haemulon aurolineatum were taken in significantly more night tows because dense day-resting schools dissociate at night when this species disperses to feed. It is well documented that grunts form resting schools on various reefs during the day (Starck and Davis 1966; Collette and Talbot 1972; Hobson 1973; Ebeling and Bray 1976; Ogden and Ehrlich 1977). At dusk, members of the school become active and undertake feeding migrations into areas near the reef which may have sandy bottom or algal cover. The dispersal of *H. aurolineatum* from dense daytime schools is reflected in the present study by changes in Morisita's index of dispersion (Elliott 1977) for day and night trawl tows. The index equals 1 for a random distribution, >1 for a contagious distribution, and <1 for a regular distribution (Elliott 1977). Day trawl tows had an index of dispersion of 5.51 which indicates a highly significant contagious distribution of *H. aurolineatum*. Night collections also had a significant contagious distribution, but the value of the index was much lower (1.44). By comparing both Morisita's index and the frequency of occurrence of *H. aurolineatum* in day and night tows, it can be inferred that tomtate disperse over the habitat during the night hours. In addition, the occurrence of tomtate in three of six night tows in the open-shelf study area provided evidence that the species leaves the sponge-coral habitat at night.

Although *Stenotomus aculeatus* occurred more frequently in night tows (79%) than in day tows (39%), the results were not significantly different. Southern porgy are daytime feeders (Harris 1979) which, as indicated by trawl results, form relatively large schools. The index of dispersion showed significant contagion in both day ($I_\delta = 4.14$) and night tows ($I_\delta = 2.43$); however, the lower night values indicate that the cohesiveness of the schools decreases at night. As a result of the greater nocturnal dispersal of this species throughout the sponge-coral habitat, the frequency of its occurrence in trawl tows increases. This accounts for the more consistent but lower catch rate at night, in comparison with day catches.

Stephanolepis hispidus showed the same pattern as *Stenotomus aculeatus* in its distribution and abundance in sponge-coral habitat tows. Planehead filefish were more aggregated during the day ($I_\delta = 3.99$) than at night ($I_\delta = 1.96$) and had a slightly higher frequency of occurrence in night trawl tows (97%) than in day collections, although the difference was statistically insignificant.

In addition to the species discussed above, several other less abundant fishes showed increased availability to night trawl tows in the sponge-coral habitat. The gadid *Urophycis earlli* was found only in night collections. Parker et al. (1979) reported *U. earlli* to be a secretive species that hid in and under artificial reef structures off the South Carolina coast. Daytime observations in winter revealed hundreds of Carolina hake under reef material (see Parker et al. 1979, fig. 10). Data from historical surveys indicate that *U. earlli* is a nocturnal species since almost all specimens collected by traps, handlines, and trawls were taken at night in the sponge-coral habitat or the rugged areas of the shelf-break (Wenner, unpubl. data). During the day, *U. earlli* probably hides under small ledges where it is unavailable to the trawl gear.

Carapus bermudensis is a nocturnal species that was unavailable to day otter trawl tows. This species spends its day residing in the respiratory tree of several species of holothurians and emerges at night to feed on near-bottom plankton (Starck and Davis 1966; Smith et al. 1981). Most bothids were encountered in night tows, probably due to these species' increased vulnerability at night.

In summary, day otter trawl catches were more variable in numerical abundance but frequently weighed more than night catches. This was due to the dense schools formed during daylight by species such as *Haemulon aurolineatum* and *Stenotomus aculeatus*. Night tows had more species because of the nocturnal availability of such species as *Apogon pseudomaculatus*, *Carapus bermudensis*, the ophidioids, etc., as well as the increased vulnerability of diurnal species such as *Holacanthus isabilita* and *Chromis enchrysurus*.

Comments on Use of Otter Trawl Nets in Sponge-Coral Habitat Surveys

Demersal trawl surveys are conducted in the northeast region of the United States to determine the species composition, distribution, and relative abundance of finfish, squids, and decapod crustaceans (Grosslein 1969). This survey has been designed so that the investigators can use some aspect of the catch per unit effort from research vessels to obtain an index of relative abundance for some groundfish stocks. This index, with appropriate adjustments, can be used (see Clark and Brown 1977) to derive regional stock-size estimates independent of the commercial catch. These, in turn, can be utilized for management decisions. In addition, some indication of the abundance of prerecruits can be obtained from the juveniles retained in the small mesh cod end liner of most research survey nets.

Although trawl gear can determine the size and relative abundance of many species that are available and vulnerable to the gear, its use to assess commercially harvested species of the sponge-coral habitat is suspect for the following reasons. First, as previously indicated, most commercially important lutjanids, sparids, and serranids are adept at avoiding the survey gear. High rise nets (otter trawls with greater vertical mouth openings) are more efficient in obtaining representative samples of these fishes, but swept-area estimates of the density of these species are unreliable. Most sponge-coral habitats have sections of small rock outcroppings and ledges where epinepheline serranids, lutjanids, and sparids aggregate. Because of possible gear destruction due to the high relief, these areas are untrawlable and catches in the remainder of the habitat show these species to be either absent or of minor importance. Trap and handline collections in untrawlable areas of this habitat document the localized abundance of these animals and indicate the importance of these species to the fish community.

Second, even with cod end liners, the ¾ Yankee and high-rise roller trawl nets fail to give indications of the abundance of prerecruits (Wenner unpubl. data). Available data indicate that the juveniles of epinepheline serranids are either spatially separated from the adults (*Mycteroperca microplepis*) or are cryptic forms which hide in cracks and crevices in this habitat (Johnson[5]). Juvenile *Rhomboplites aurorubens* are available and vulnerable to the gear during late summer months on 30-40 m sampling sites. This is the only species of the commercially important complex that is taken with any regularity.

Thus, otter trawl gear is neither effective in predicting recruitment of most commercially important species, nor reliable in providing accurate abundance estimates of these species. In addition, the physical habitat may sustain considerable damage caused by the bottom trawl net.

The ¾ Yankee trawl net effectively covers a much wider area of the bottom than the measured sweep (8.7 m) due to the configuration of the otter doors, ground cables, and bottom leg lines. Although this arrangement cannot increase the actual spread of the net beyond the headrope length, the passage of these cables over the substrate creates a disturbance that serves to herd fish in the path of the net (Baranov 1969). This net does, however, damage the sponge-coral habitat by shearing off sponges, soft corals, bryozoans, and other attached invertebrates. The 56 trawl tows made in the sponge-coral habitat for this study collected 2,351 kg of attached invertebrates (including sponges, soft corals, tunicates, bryozoans, and hydroids) yielding an average 42 kg/tow. This is only the amount of bottom material actually removed from the habitat. An estimate of the total amount of bottom destroyed by the doors, ground cables, and leg lines cannot be ascertained from the current study.

Personal observations and interviews with commercial fishermen attest to the productivity of the sponge-coral habitat. Most studies indicate the importance of habitat availability and space in determining the abundance and diversity of reef fishes (Emery 1978). With this in mind, and given the knowledge that 1) the use of the ¾ Yankee trawl net reduces the amount of attached invertebrate growth (the amount damaged by doors and ground cables is presently not quantifiable); 2) the places where the invertebrates had been attached may be sanded over and rendered unsuitable for recolonization; and 3) the removal of these attached invertebrates reduces refugees for decapods, polychaetes, etc., that are food items for *Centropristis striata* and other benthic feeders, one must conclude that the continued use of this trawl net reduces the amount of productive fish habitat. For these reasons, in addition to the ineffectiveness of the gear in sampling commercially important species, alternate nondestructive methods, such as direct observations or the use of mark-recapture techniques with trap catches, should be employed in assessment surveys of the commercially important species of this habitat.

[5]G. David Johnson, South Carolina Wildlife and Marine Resources Dept., P.O. Box 12559, Charleston, SC 29412, pers. commun., 1981.

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REPRODUCTIVE BIOLOGY OF THE BLUELINE TILEFISH, *CAULOLATILUS MICROPS*, OFF NORTH CAROLINA AND SOUTH CAROLINA[1]

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ABSTRACT

Blueline tilefish, *Caulolatilus microps*, were obtained by hook and line fishing and port sampling operations off North Carolina and South Carolina from 1972 to 1977. *Caulolatilus microps* spawn off the Carolinas from April through October, with peak activity off North Carolina in May-June and September-October. Multiple spawnings by individual females were indicated by multimodel size distributions of ova; this is complemented by the continuous production of spermatozoa in testes, which is facilitated by dynamic spermatogenic tubules. Fecundity is best predicted by fish weight: ln Fecundity = 0.016 + 1.832 ln Weight. Fecundity estimates ranged from 0.2 million ova for a 412 mm TL (0.82 kg) fish to 4.1 million ova for a 736 mm TL (4.85 kg) fish. Females attained sexual maturity between 425 and 450 mm TL (age IV-V). Males showed pronounced testicular development after age V (500 mm TL). Females were more abundant from 300 to 500 mm TL; the sex ratio was 1:1 between 500 and 600 mm TL; males predominated in size classes greater than 600 mm TL. Protogynous sex reversal in three juvenile specimens (156-202 mm TL) was indicated by transitional gonads or testes with residual oocytes. Previtellogenic oocytes in 8 of 42 mature males (436-700 mm TL) further suggest protogyny, although no adult fish with transitional gonads were observed. Whether blueline tilefish are strictly juvenile or functional hermaphrodites has yet to be determined.

The blueline tilefish, *Caulolatilus microps* Goode and Bean, is a semitropical demersal branchiostegid that constitutes a significant component of the deepwater grouper-snapper fishery off North Carolina and South Carolina (Huntsman 1976). It inhabits the outer continental shelf, shelf edge, and upper slope (70-235 m) from Cape Charles, Va., to Key West, Fla., and in the Gulf of Mexico from Pensacola, Fla., to Campeche, Mexico (Dooley 1978).

In 1972 scientists at the Southeast Fisheries Center of the National Marine Fisheries Service (NMFS) began studying the biology, community relationships, and population dynamics of the offshore demersal (reef) fishes off the southeastern United States, ultimately to provide effective management of this fishery (Huntsman 1976). The reproductive biology of blueline tilefish was investigated as part of that program, and is herein described with respect to 1) spawning seasonality, 2) descriptive gonadogenesis, 3) fecundity, 4) age/size of sexual maturity, 5) sex ratio with size, and 6) sexual transition.

The reproductive biology of *C. microps* is previously undescribed. Dooley (1978) reported the capture of ripe females in January and May through September off North Carolina. Brief notes on reproduction for other branchiostegids suggest protracted spawning seasons for *C. princeps* (Fitch and Lavenberg 1971), *C. affinis* (Dooley 1978), *Lopholatilus chameleonticeps* (Freeman and Turner 1977; Grimes[4]), and *Branchiostegus japonicus japonicus* (Hayashi 1977). Dooley and Paxton (1975) related the presence of several size classes of ova in maturing *B. wardi* and *B. serratus* to multiple spawning and found anomalous sex ratios within size classes. Pelagic eggs and larvae of *Caulolatilus* sp. and *L. chameleonticeps* have been collected off the Carolinas and in the northwest Atlantic (Freeman and Turner 1977; M. Fahay[5]).

MATERIALS AND METHODS

Blueline tilefish were captured over rugged precipitous bottoms as well as gently sloping sections of the shelf edge (Fig. 1). Specimens were obtained by hook and line fishing with electric reels and rods from

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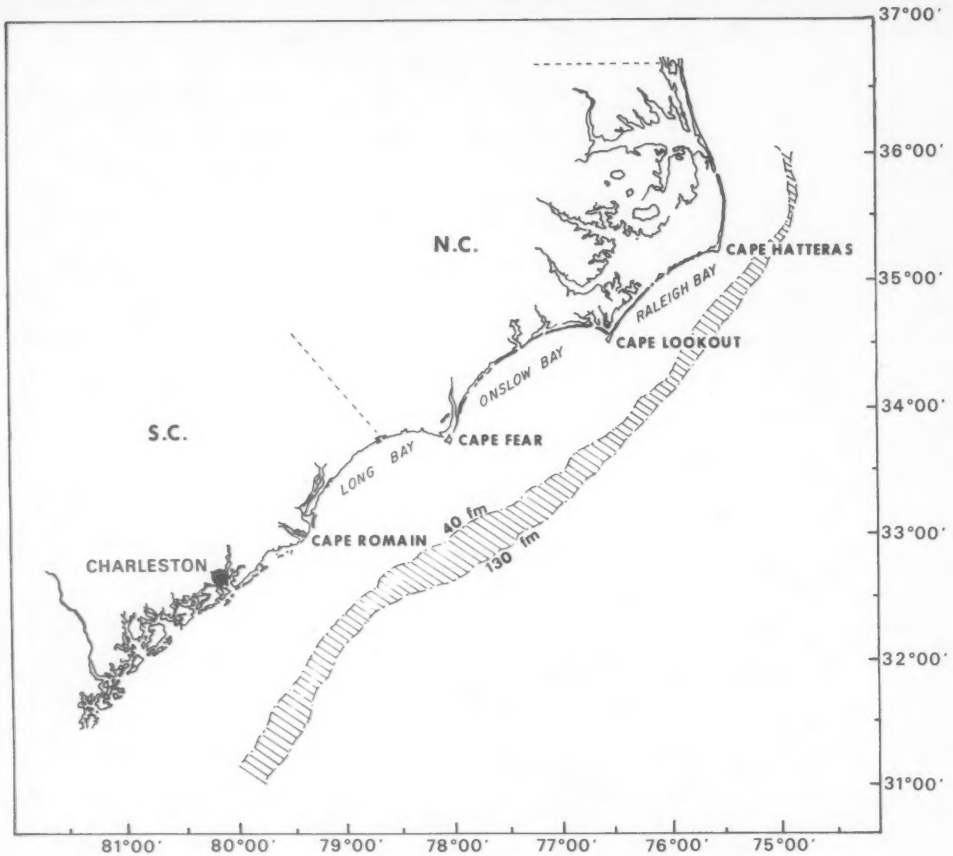

FIGURE 1.— Distribution of *Caulolatilus microps* off North Carolina and South Carolina (noted by hatch marked area).

1972 to 1977 in the northern and central portions of Onslow Bay aboard the RV *Onslow Bay* (NMFS). Fishing was most successful when baits were maintained as close to the bottom as possible. Total length (TL, mm) and total weight (W, g) were recorded for each fish, gonads excised and stored in 10% Formalin[6] and otoliths removed and stored in glycerine. Sampling of headboats fishing out of North Carolina and South Carolina ports provided ancillary records of total length and total weight, and samples of gonads and otoliths.

A gonosomatic index (GSI) was calculated according to the formula

$$GSI = \frac{GW}{W} \times 100$$

where GW = preserved gonad weight (0.1 g) and W = total body weight (g). GSI was used to determine spawning seasonality and sexual maturity.

Sex was determined by gonad examination since blueline tilefish apparently exhibit no sexually dimorphic characteristics. Ovaries and testes were staged macroscopically and histologically after preservation in 10% Formalin (Tables 1, 2). Ova stages corresponded to those described by Moe (1969) for red grouper, *Epinephelus morio*: oogonia, 2-8 μ; stage I, early oocytes, 20-50 μ; stage II, previtellogenic oocytes, 40-170 μ; stage III, early vitellogenic oocytes, 110-260 μ; stage IV, active vitellogenic oocytes, 215-650μ; stage V, mature ova, 735-910 μ

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

with 140-196 μ oil globule. Spermatogenic stages were analogous to those described by Moe (1969) for red grouper and Hyder (1969) for *Tilapia*. Routine histological methods were used for slide preparations from Formalin-fixed gonads.

Frequency distributions of ova diameters were plotted by gonad stage to determine individual spawning patterns. Representative females were selected for each ovarian stage. The diameter of 50 ova from each occurring stage (previtellogenic, early vitellogenic, active vitellogenic, and mature oocytes) were measured from each sample using a gridded petri dish and a magnification of 70×. A ratio of the four stages was then determined by reducing the magnification to 20× and counting two or more entire grids until about 500 ova were counted. This ratio was reduced to a base of 200 and combined with ova diameter frequencies per stage data using the ratio

$$\frac{\text{frequency of ova stage}}{200} \times \frac{\text{ova diameter frequency}}{50}$$

to determine the relative frequency of each size group.

Well-Developed and Ripe ovaries from fish captured from April through September were used for fecundity estimates. One ovary randomly selected from each pair was weighed to the nearest 0.1 g. The ova were teased free of the ovarian tunic. Two subsamples were removed and all vitellogenic ova (stages III-V; determined by relative size and opacity of cytoplasm) were counted. The sample and subsamples were oven dried and weighed to the nearest 0.001 g. The formula

$$Y = \frac{(W)\ (w_i)}{(W_i)\ (w)}\ y$$

was used to estimate fecundity, with Y = total number of eggs in both ovaries, W = wet weight of both ovaries, W_i = wet weight of selected ovary, w_i = total dry weight, w = total dry weight of subsamples, and y = number of ova in subsamples (Manooch 1976).

TABLE 1.—Developmental stages of *Caulolatilus microps* ovaries.

Maturity stage	External appearance	Ova composition
Immature (stage 1) (>250 mm TL)	Small, maroon, sausage to teardrop shaped hollow organs.	Ovigerous lamellae composed of dense aggregations of undifferentiated oogonia and primary oocytes.
Resting (stage 2)	Flaccid triangular sacs with translucent tunic and dark reddish internal mass.	Primarily early and previtellogenic oocytes with <1% early vitellogenic oocytes.
Developing (stage 3)	Ovary becomes increasingly rotund while maintaining a basic triangular shape; yellowish orange appearance due to granular ovigerous mass. tunic becomes more transparent, and ova are discernable.	Previtellogenic oocytes numerically dominant with some early and active vitellogenic oocytes. Well-developed ovaries contain an increasing number of vitellogenic oocytes evenly distributed over a large size range (215-650 μ).
Well-Developed (stage 4)	Ovarian tunic becomes nearly transparent yellowish ova densely packed and discernable.	Vitellogenic oocytes predominant and evenly distributed over a large size range (215-650 μ).
Ripe (stage 5)	May-August: Greatly distended, bulbous and occupying more than 1/3 of the peritoneal cavity; very light orange to white in color; 2-4% body weight. Ova clearly visible through delicate, nearly transparent tunic.	Broad size distribution of vitellogenic oocytes, with a mode of very large (420-640 μ) vitellogenic oocytes together with stage III and small (215-400 μ) stage IV oocytes. Mature oocytes (785-910 μ) characteristically contained in lumen, free of ovigerous lamellae.
	September-October: Ovaries comparatively smaller, firm, more triangular though rotund; 1-2.4% body weight.	A mode of large stage IV oocytes with stage V oocytes present and relatively few small (215-400 μ) stage IV oocytes.
Recently Spent-Redeveloping. (stage 6-3)	Resemble deflated early developing ovaries; distinguished by inflamed ventral, posterior portion, otherwise cream colored.	Stage III and small stage IV oocytes occur together with some very large stage IV and stage V oocytes, the latter often in an atretic state.
Spent (stage 6)	Flaccid, reduced in size; muscular tunic contracting and becoming firm, inflamed.	No evidence of vitellogenesis; stage IV and V oocytes are atretic; a few stage III oocytes occur.

TABLE 2.—Developmental stages of *Caulolatilus microps* testes.

Maturity stage	External appearance	Spermatogenic activity
Immature/Resting	Basically threadlike maroon organs with slight laterally compressed expansion posteriorly above sperm duct.	Spermatogenic tubules generally inactive, though spermatozoa may occur in lumen of spermatogenic tubules and collecting tubules.
Developing	Maroon, thin, elongate, laterally compressed, with widest portion directly above sperm ducts, tapering rapidly to filamentous anterior projection.	Spermatogenic tubules contain crypts at all developmental stages with spermatozoa collecting in the lumen and collecting tubules.
Well-Developed	More robust, triangular to nearly cornucopia shaped, tapering anteriorly. Maroon to creamy off-white color.	Extensive collections of spermatozoa in expanded lumens of actively developing spermatogenic tubules, with channeling of spermatozoa into medial collecting tubules.
Ripe	No running ripe testes observed	

Juvenile specimens were obtained for gonadal analysis from the Field Museum of Natural History, Chicago, Ill., and the Institute of Marine Science, University of North Carolina, Morehead City, N.C.

RESULTS

Gonadal Development

The paired ovaries of *C. microps* are suspended below the swim bladder by mesovarium in the most posterior portion of the body cavity. The mesovarium extends the length of the ovary and contains the ovarian arteries. Oogenesis and vitellogenesis occur within the ovigerous lamellae which are distributed evenly and project laterally and medially from the tunica albuginea. The absence of lamellae from a narrow band in the ventral portion of the ovary forms an ovocoel. This facilitates ovarian expansion and collection of ripe ova released from the lamellae prior to extrusion through the common oviduct (Moe 1969).

Testes of blueline tilefish are solid, smooth textured, compressed laterally, and relatively more elongate than ovaries. They are suspended from the swim bladder by the mesorchium, which has a wide base of attachment along the medial surface. Each testis enters the urinary papilla by a separate sperm duct.

The structure and developmental pattern of the testes are similar to that described by Smith (1965) as tubular. The primary spermatogenic units are radial spermatogenic tubules and spermatogenic crypts. In cross section, the spermatogenic tubules are essentially a ring, one spermatogonium or one spermatogenic crypt thick (Fig. 2). An elastic connective tissue, the Sertoli cells, encapsulates and maintains the integrity of the tubules and the individual developing crypts. It presumably serves as the site of steroidogenesis (Lofts 1968; Hoar 1969). Development proceeds at varying rates within each spermatogenic tubule, analogous to that in the ovigerous lamellae, so that active spermatogenic tubules usually contain crypts at all stages of development (Fig. 3). Spermatids were the most advanced stage observed within a crypt. Spermiogenesis, the morphogenesis of spermatid to spermatozoa, occurred around the time of passage from crypt to the lumen of the spermatogenic tubule.

Whereas in many fishes the interstitial tissue separating the developing tubules breaks down at later stages of development resulting in extensively

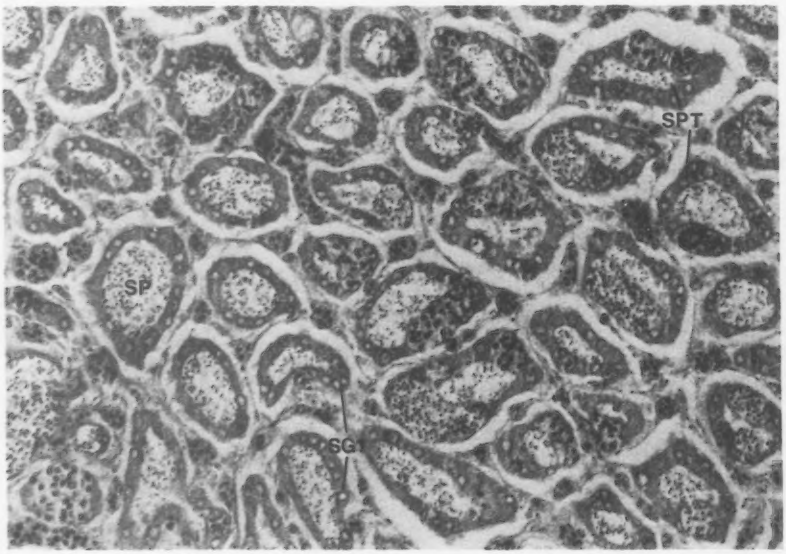

FIGURE 2.—Cross section of Early-Developing testes from a 530 mm TL *Caulolatilus microps* collected 15 March 1977. Note radial spermatogenic tubules (SPT) composed principally of primary spermatogenia (SG1) with few developing crypts, and the presence of spermatozoa (SP) in the lumen of the spermatogenic tubules (Haematoxylin × 200).

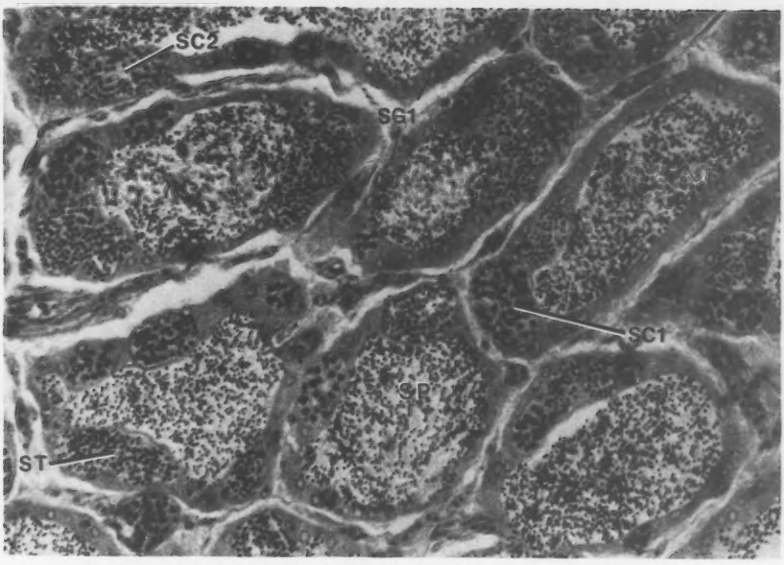

FIGURE 3.—Cross section of Developing testes from a 664 mm TL *Caulolatilus microps* captured 9 September 1974. Note spermatogenic tubules composed of the spectrum of developing crypt stages, with primary (SG1) spermatogonia; primary (SC1) and secondary (SC2) spermatocytes; spermatids (ST); and collections of spermatozoa (SP) in the lumen (Haematoxylin and eosin × 200).

packed sinuses of spermatozoa, the spermatogenic tubules of *C. microps* maintain their integrity. Drainage of spermatozoa from the testes results from the dynamic nature of the tubules. In the course of their development, they migrate medially from the lateral epithelium. Several observations support this hypothesis. In an early-developing male captured in May (Fig. 4), the lateral spermatogenic tubules are undeveloped and inactive with small amounts of spermatozoa in the lumen. Those adjacent to the dorsomedial portions of the testes are also generally inactive but contain larger collections of spermatozoa. This suggests that longevity of spermatogenic tubules exceeds one season and that spermatogenic tubules generate from the peripheral interstitium (Lofts 1968). The spermatogenic tubules adjacent to the dorsomedial connective tissue in developing testes are generally the most well developed, and can be seen merging with the medial collecting tubules (Fig. 5). The collecting tubules have boundary cells that are essentially connective tissue, and contain only spermatozoa. The spermatogenic tubules can be distinguished, since they are bordered by active spermatogenic crypts. Testicular drainage is thus accomplished by a dorsomedial migration of spermatogenic tubules and their merging with and releasing of spermatozoa into the collecting tubules. The collecting tubules channel the spermatozoa posteriorly and ventrally into the separate sperm ducts.

Spawning Seasonality

Caulolatilus microps spawn off North Carolina and South Carolina between April-May and September-October. Monthly mean GSI values for 138 females and 101 males captured off North Carolina exhibited peaks in May and September (Fig. 6). Early-Developing ovaries were predominant from February through April. High GSI values in May corresponded to the greatest incidence of Well-Developed and Ripe females (Fig. 7). The lower mean GSI values observed in June, July, and August corresponded with a diversity of gonad stages including Early-Developing, Well-Developed, Ripe, and Recently Spent-Redeveloping ovaries. Ovaries were again synchronously Well-Developed or Ripe in September though considerably smaller than gonads observed in May and June. Low GSI values from November through March reflect a period of gonad

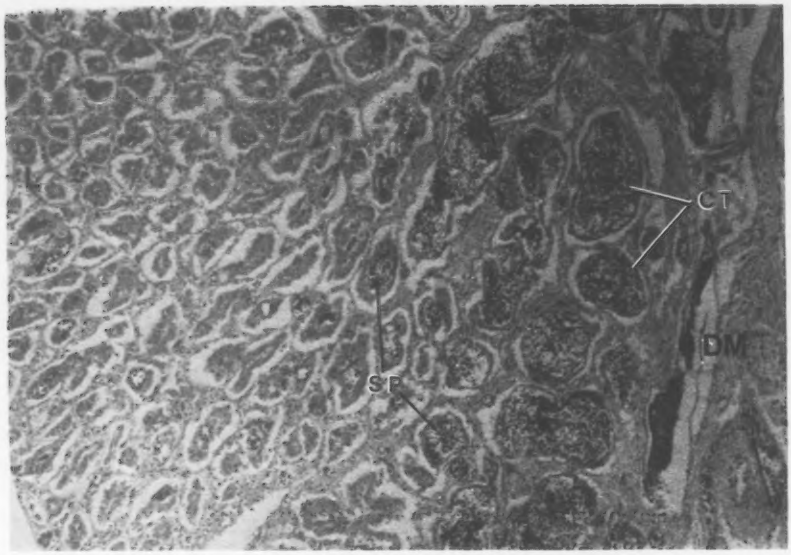

FIGURE 4.—Cross section of Resting testes from a 410 mm TL *Caulolatilus microps* collected 15 March 1977. Note undeveloped state of lateral (L) spermatogenic tubules and increased collections of spermatozoa (SP) in spermatogenic tubules and collecting tubules (CT) located along dorsomedial (DM) region (Haematoxylin and eosin × 78).

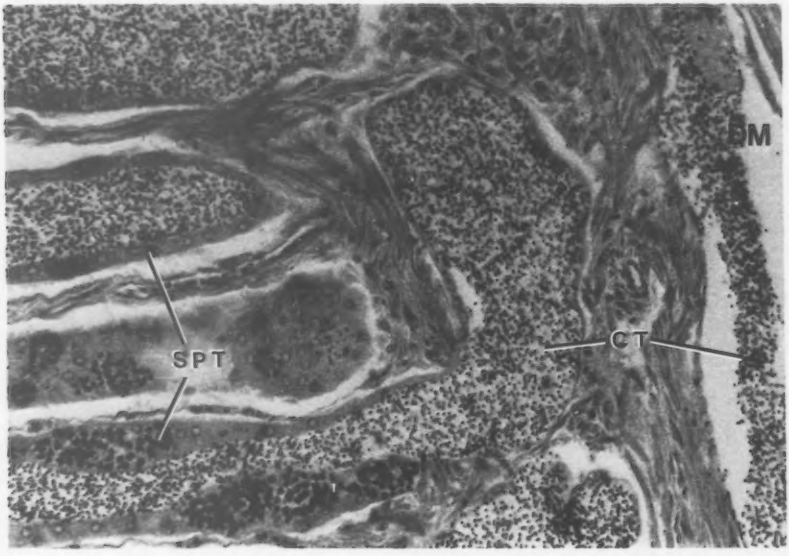

FIGURE 5.—Cross section of Developing testes from a 664 mm TL *Caulolatilus microps* collected 9 September 1974. Note spermatogenic tubules (SPT) composed of active crypts merging with and channeling spermatozoa into collecting tubules (CT) which occur along the dorsomedial (DM) tunica albuginea (Haematoxylin and eosin × 256).

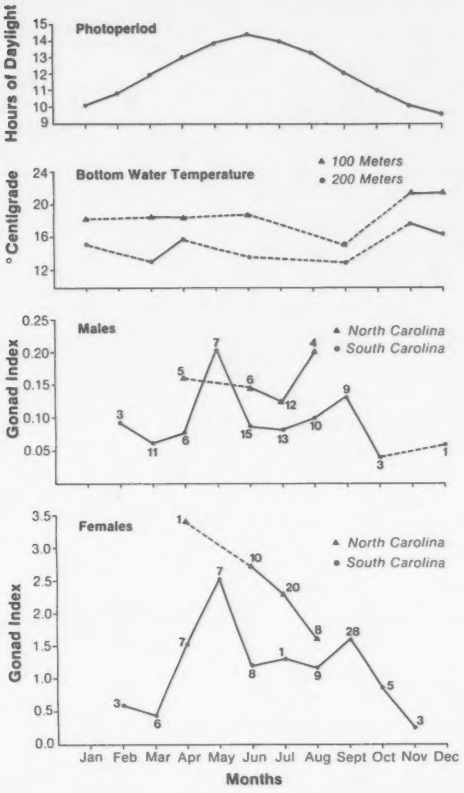

FIGURE 6.—Monthly mean gonad index values for male and female *Caulolatilus microps* from North Carolina and South Carolina, mean bottom temperatures off Beaufort, N.C. (Stefansson and Atkinson 1967), and photoperiod.

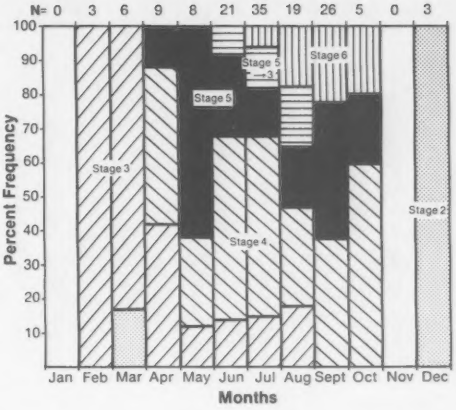
N= 0 3 6 9 8 21 35 19 26 5 0 3
Percent Frequency
Stage 3
Stage 5
Stage 6
Stage 4
Stage 2
Jan Feb Mar Apr May Jun Jul Aug Sept Oct Nov Dec
Months

FIGURE 7.—Percent frequency histogram of gonad developmental stages observed each month for female *Caulolatilus microps* from North Carolina and South Carolina.

regression and early development. Ripe females were captured off South Carolina during April and July, which could indicate a more continuous or three-peaked spawning season. Monthly mean GSI as well as mean standard length were greater for females off South Carolina, but data are too limited to draw any further conclusions.

Analysis of ova development within individual ovaries suggested that blueline tilefish are multiple spawners (Fig. 8). Ovaries considered Resting characteristically contained primary oocytes and previtellogenic oocytes. Early-Developing ovaries showed a progression of early vitellogenic oocytes developing from the residual stock. Well-Developed ovaries in late April contained a mode of late vitellogenic oocytes cooccurring with previtellogenic and early vitellogenic oocytes (Fig. 9). Ripe females from May and June exhibited modes of previtellogenic oocytes, early vitellogenic oocytes, late vitellogenic oocytes, and mature eggs. This indicated continuous development from the residual stock of oocytes occurred when spawning was imminent. Early vitellogenic ova are predominant in Spent-Redeveloping ovaries and cooccur with residual mature, atretic mature, and late vitellogenic oocytes. Late vitellogenic oocytes were again the predominant oocytes in Well-Developed ovaries during September. There was also a decreased proportion of early vitellogenic oocytes in comparison with Well-Developed gonads from May.

Males accommodate the protracted season of oogenesis by maintaining a constant state of development during the spawning season. The two peaks in GSI of testes coincided with those observed for ovaries (Fig. 6). Testes contained some spermatozoa in all months sampled and observed histologically, while those from April through September generally contained large quantities of spermatozoa in the collecting tubules. However, we never captured any males with free-running milt.

Fecundity

We estimated the fecundity of blueline tilefish from three periods during their spawning season. Fecundity ranged from 210,000 ova (412 mm TL) to 3,220,000 ova (637 mm TL) for 18 fish captured from April to early June (Fig. 10). Fecundity was significantly correlated with both length and weight:

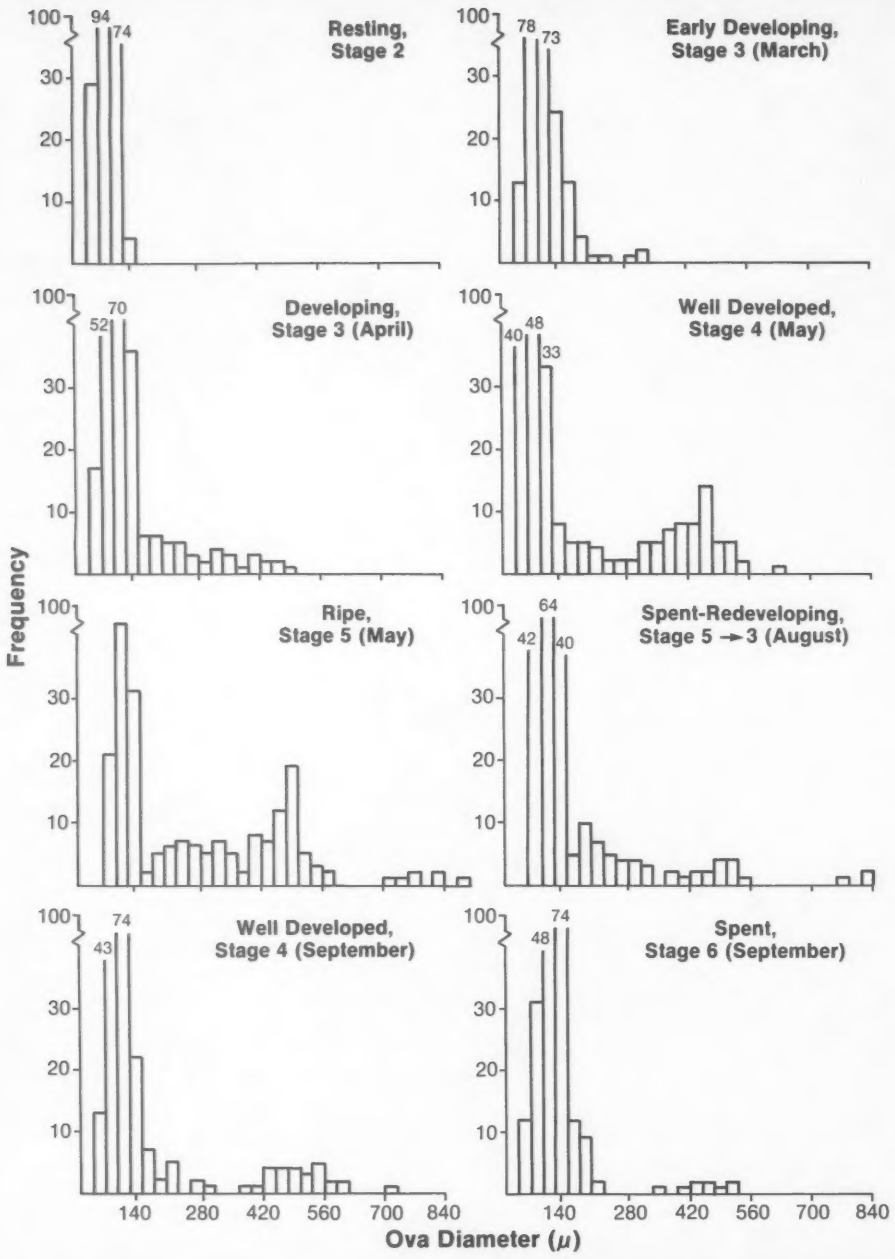

FIGURE 8.—Ova diameter frequency distributions for designated ovarian developmental stages for female *Caulolatilus microps* from North Carolina.

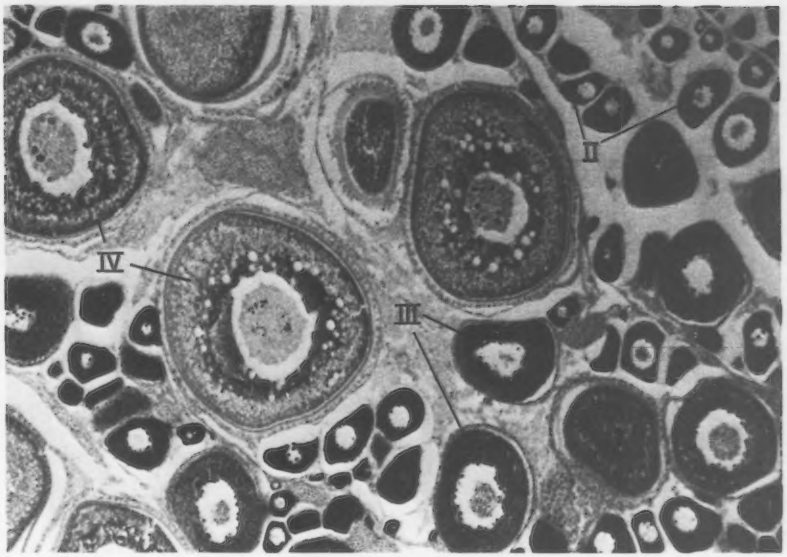

FIGURE 9.—Cross section of Well-Developed ovary from a 515 mm TL female *Caulolatilus microps* (21 April 1977) with lamellae composed of residual stock previtellogenic oocytes (II), early vitellogenic oocytes (III), and late vitellogenic oocytes (IV) (Haematoxylin and eosin × 63).

$$\ln \text{Fecundity} = 8.830 + 0.00986 \text{ Total length}$$
$$r^2 = 0.74, \text{ and}$$
$$\ln \text{Fecundity} = 0.016 + 1.832 \ln \text{Weight}$$
$$r^2 = 0.78.$$

Fecundity for 14 Ripe females captured in July basically agreed with the above fecundity relationship; the estimates ranged from 196,000 (436 mm TL) to 4,107,035 ova (736 mm TL). The estimated fecundity of 12 Well-Developed and Ripe females from September decreased approximately one-third to one-half. The production of vitellogenic ova appears greater during the late spring-early summer spawning peak than the early fall peak. However, insufficient data on the frequency of spawnings by individuals within age/size groups and the number of eggs released preclude further refinement of individual annual fecundity estimates.

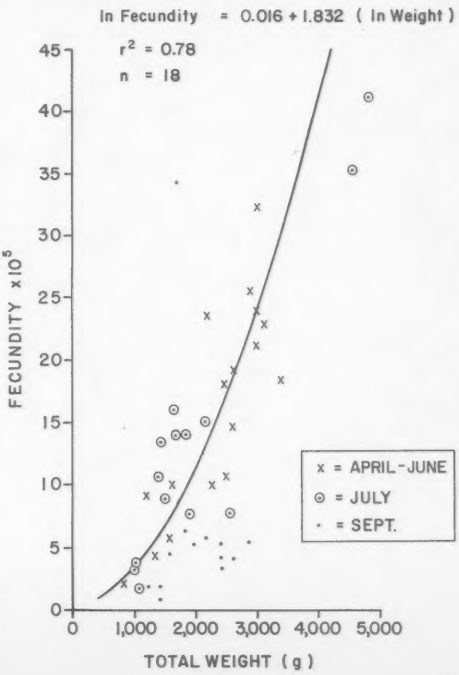

FIGURE 10.—Fecundity-weight relationship for *Caulolatilus microps* collected in April to June. Fecundity estimates are plotted for fish captured in July (South Carolina) and September (North Carolina).

Sexual Maturity

Maturity of females, defined as the size at which >50% of the individuals were gonadogenically active, occurred between 425 and 450 mm TL (Table 3) which is typically a 4- or 5-yr-old fish (Ross and Huntsman 1982). One of three age III females (387-421 mm TL), 50% of the age IV ($n = 8$; 427-506 mm TL), 73% of the age V ($n = 15$; 430-546 mm TL), and 100% of the age VI+ females were mature. The pattern of ovarian development corroborated the macroscopic maturity analysis. Relative gonad weight increased with total length after initial steep increases in relative gonad size between 400 and 500 mm TL. Mean GSI and maximum relative gonad weights were consistently greater for females captured off South Carolina than those captured off North Carolina, although the biological reason for this is unknown.

Male *C. microps* show little gross testicular development under 500 mm TL (Table 3). Macroscopically, 50% were considered immature between 500 and 525 mm TL and 100% attained maturity above 600 mm TL. No age IV ($n = 4$; 436-453 mm TL) and only 12.5% of the age V males ($n = 8$; 485-574 mm TL) were considered mature, and a majority (62.5%) had not matured until age VI ($n = 8$; 520-556 mm TL). The initial and most pronounced increase in relative testis size occurred in males >500 mm off North Carolina and males >600 mm off South Carolina. Histological examination of testes from males 390-500 mm TL ($n = 11$) revealed spermatogenesis and collections of spermatozoa in fish macroscopically considered immature. These testes were very small (<0.08% body weight) and maroon in color. We could not determine whether this represented precocious development or functional maturity.

TABLE 3.—Percentage of sexually mature female and male *Caulolatilus microps* from North Carolina and South Carolina.

Total length	Females		Males	
	N	Percent mature	*N*	Percent mature
250-300	3	0		
301-325				
326-350	1	0		
351-375	2	0		
376-400	5	20.0	1	0
401-425	11	45.5	1	0
426-450	8	75.0	4	0
451-475	11	81.8	3	0
476-500	11	90.9	5	20.0
501-525	24	100.0	8	50.0
526-550	24	100.0	9	77.8
551-575	18	100.0	9	77.8
576-600	8	100.0	8	87.5
601-625	13	100.0	7	100.0
626-650	11	100.0	13	100.0
650+	4	100.0	41	100.0

Sex Ratio and Sexual Transition

Males outnumbered females in the combined North Carolina and South Carolina collections (195 to 176), but this was not significantly different from a 1:1 ratio ($\chi^2 = 0.97$). However, sex ratios become skewed when size (Table 4) or age (Table 5) are considered. Females were more numerous between 300 and 500 mm TL, and in several cases there were significant deviations from 1:1. Between 500 and 600 mm TL

TABLE 4.—Frequency of male and female *Caulolatilus microps* from North and South Carolina within 25 and 100 mm TL intervals, with Chi-square values assuming a 1:1 sex ratio.

Length	Male	Female	Percent female/25 mm	χ^2	Percent female/100 mm	χ^2
101-200	3	1			25	1.0
201-300		1			100	
301-325						
326-350		1	100		88	5.4*
351-375		1	100			
376-400	1	6	86	3.57		
401-425	1	6	86	3.57		
426-450	7	12	63	1.32	67	9.89*
451-475	6	20	77	7.54*		
476-500	14	19	58	0.75		
501-525	20	23	53	0.21		
526-550	15	18	55	0.27	52	0.32
551-575	19	22	54	0.22		
576-600	18	16	47	0.12		
601-625	19	16	46	0.26		
626-650	16	8	33	2.67	30	16.9*
651-675	20	3	13	12.57*		
676-700	15	2	12	9.94*		
701-725	11	0	0			
726-750	5	1	17		9	15.6*
751-775	3	1	25			
776-800	2	0	0			

*$P \leq 0.05$.

TABLE 5.—Frequency of male and female *Caulolatilus microps* from North and South Carolina within age groups with Chi-square values assuming 1:1 sex ratio.

Age	Females	Males	X^2
II	1		1.8
III	3	1	
IV	16	4	7.2*
V	26	15	2.95
VI	16	9	1.96
VII	11	7	0.89
VIII	11	16	0.93
IX	7	4	0.82
X	4	12	4.00*
XI	1	3	1.0
XII	0	6	6.0*
XIII	0	2	
XIV	0	2	3.57
XV	1	2	

*$P \leq 0.05$.

the sex ratio was essentially 1:1. In fish >600 mm TL, males became increasingly and significantly more abundant. Similarly, females outnumbered males in ages III through VII while males became predominant for ages X through XV.

Histological evidence from four juvenile blueline tilefish indicated prematurational sex reversal. The gonad from a 186 mm TL specimen was ovarian and composed of basophilic oogonia with some primary oocytes (Fig. 11). The remaining three specimens had gonads which exhibited progressive stages of sex reversal. The earliest stage (202 mm TL) was predominantly ovarian with an acidophilic germinal testicular mesothelium proliferating through the ovigerous lamellae from the dorsomedial connective tissue (Fig. 12). The proliferating mesothelium contained primary spermatogonia and would be the site of steroidogenesis, inducing atresia and the recycling of ovarian elements (Hoar 1969). Gonads of two specimens (178 and 184 mm TL) in advanced stages of sex reversal had differentiated into the basic testicular components with spermatogenic tubules present and spermatogenesis proceding (Figs. 13, 14). Both specimens revealed evidence of a previous ovarian stage in the form of atretic structures, residual oocytes, or proliferating testicular mesothelium along the peripheral epithelium. These specimens were all captured in March and were within the size range predicted for *C. microps* after one year of growth (Ross and Huntsman 1982). Residual oocytes were also observed in 8 of 41 developing testes from adult males (Fig. 15). These fish were 430-700 mm TL and had solid testes which exhibited no other remnant ovarian structures.

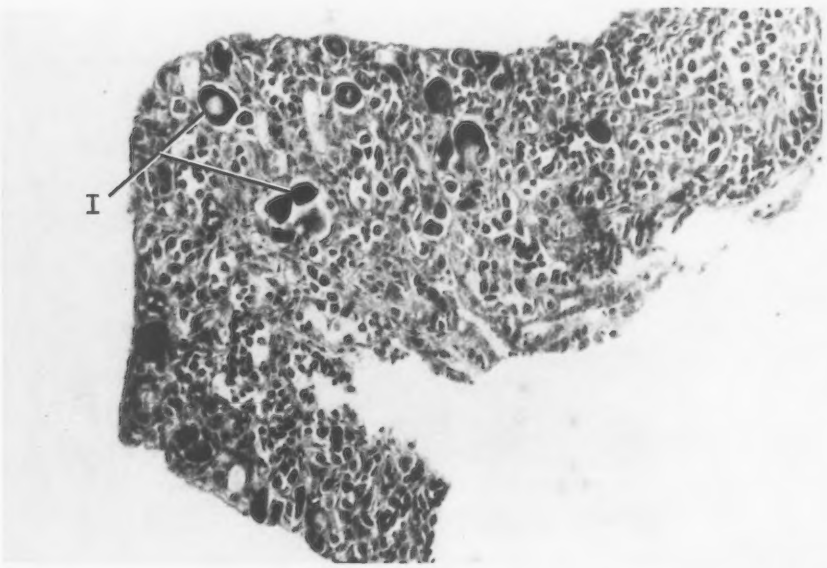

FIGURE 11.—Cross section of ovary from a juvenile 186 mm TL *Caulolatilus microps* collected 13 March 1961 with oogonia and primary oocytes (I) (Haematoxylin and eosin × 200).

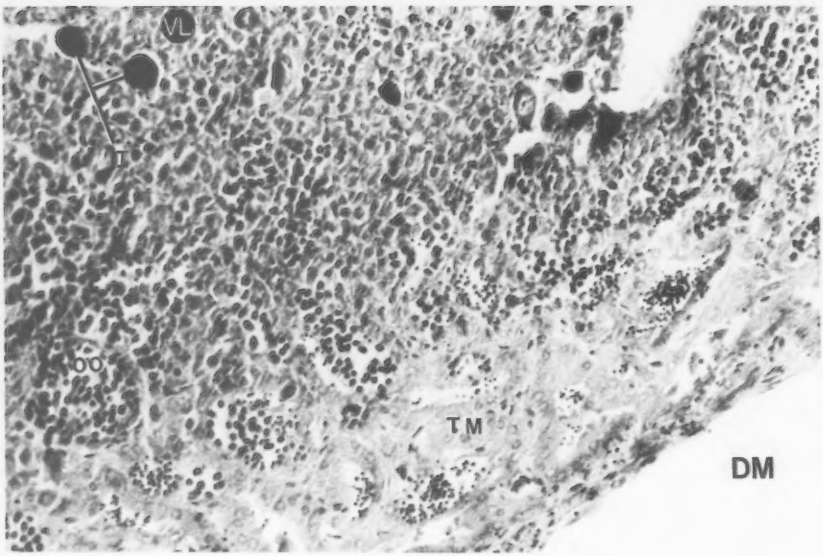

FIGURE 12.—Cross section of gonad from a juvenile 202 mm TL *Caulolatilus microps* collected 13 March 1961. Note occurrence of oogonia (OO) and primary oocytes (I) along ventrolateral region (VL) with proliferating testicular mesothelium (TM) originating from dorsomedial areas (DM) (Haematoxylin and eosin × 200).

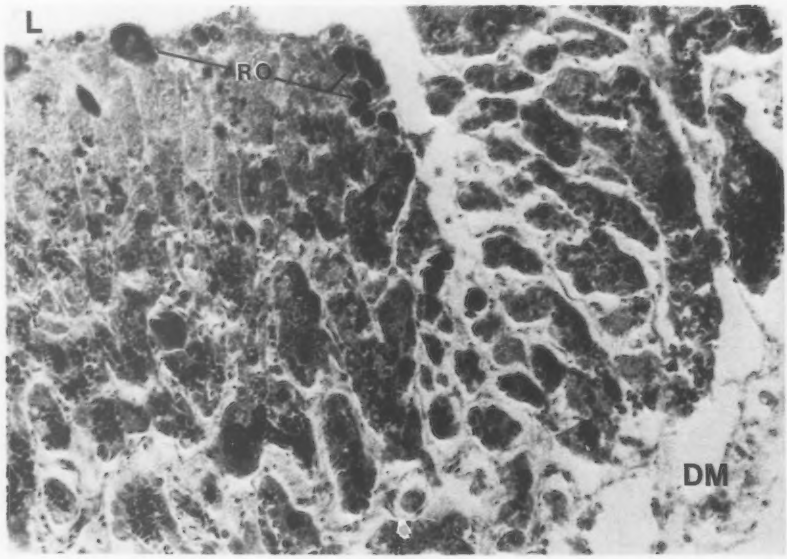

FIGURE 13.—Cross section of gonad from a juvenile 184 mm TL *Caulolatilus microps* collected 13 March 1961. Note spermatogenic tubules composing dorsomedial region (DM) and residual oocytes along lateral (L) gonadal margin (Haematoxylin and eosin × 200).

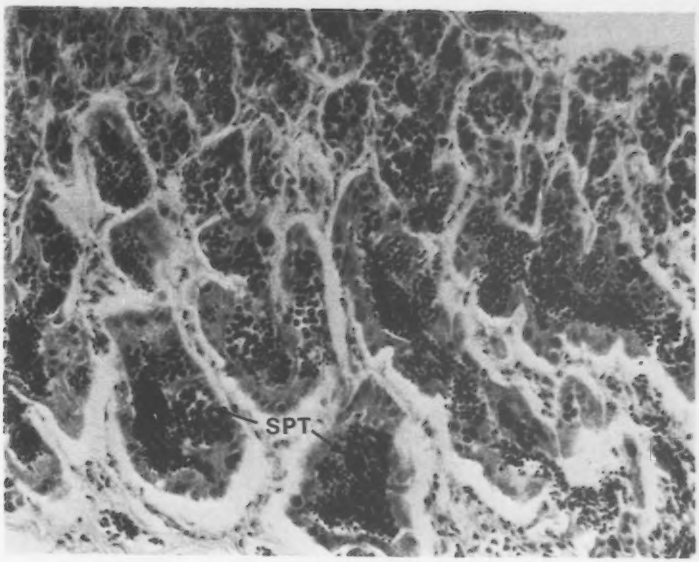

FIGURE 14.—Cross section of gonad from a juvenile 184 mm TL *Caulolatilus microps* collected 13 March 1961. Note in this closeup of previous gonad the well-defined spermatogenic tubules (SPT) (Haematoxylin and eosin × 400).

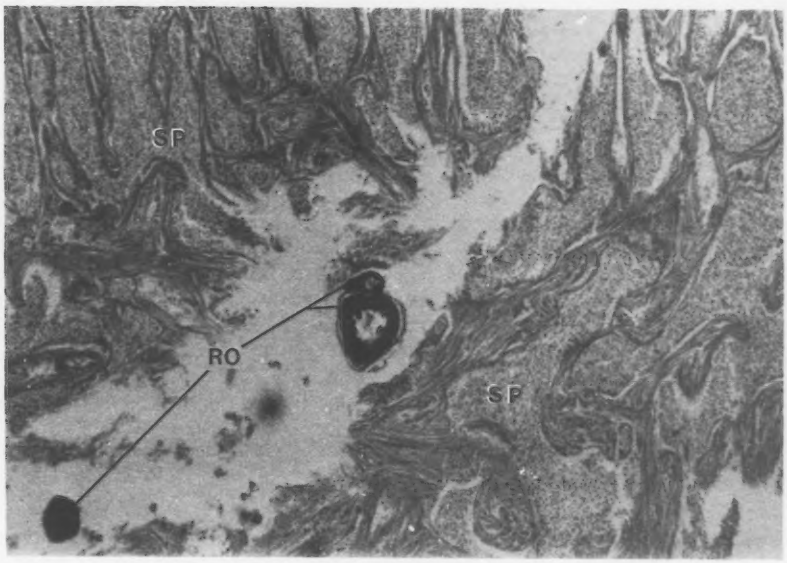

FIGURE 15.—Cross section of Well-Developed testes from a 562 mm TL (*'aulolatilus microps* captured 22 April 1977. Note extensive collection of spermatozoa (SP) and occurrence of residual previtellogenic oocytes (RO) (Haematoxylin and eosin × 78).

DISCUSSION

The initiation of gonadogenesis in blueline tilefish during March and April and the termination in September-October coincide with the periods of rapidly increasing and decreasing photoperiods (Fig. 6). This is a more conservative environmental cue than temperature when considering the shelf edge habitat. Temperature fluctuations are not necessarily seasonal, but also subject to cold-water intrusions from outer continental shelf bottom waters and meanderings of the axis of the Gulf Stream (Stefansson and Atkinson 1967). The initiation of gonadal development has also been correlated with photoperiod for the cooccurring red porgy, *Pagrus pagrus*, (Manooch 1976). The protracted spawning of vermilion snapper, *Rhomboplites aurorubens*, was correlated with both photoperiod and water temperature (Grimes and Huntsman 1980); however, its occurrence over the continental shelf increases its susceptibility to seasonal temperature variation.

Blueline tilefish ovaries seasonally undergo a progressive maturation of residual stock oocytes to vitellogenic state with several modes generated and no sharp distinctions between residual and maturing eggs. The multimodal size distribution of oocytes observed is characteristic of fishes that spawn several times during a protracted spawning season (Clark 1934; Warner 1975a; Grimes and Huntsman 1980). Off North Carolina it appears that most *C. microps* spawn during May-June and September-October. The capture of large females (>600 mm TL) that were Ripe in July and August might indicate more frequent spawning by larger fish. The generally larger females captured off South Carolina might spawn earlier and more frequently than those off North Carolina, although data supporting this conclusion are incomplete. The continuous developmental pattern of male testes would certainly accommodate protracted spawning by females.

If local spawning is directed toward the maintenance of regional populations (Marshall 1966), the production of several batches of eggs during a protracted spawning season should improve chances of concurrence with favorable environmental conditions. Of particular relevance to *C. microps* spawning are the influence and extent of transport of eggs and larvae by the Florida Current (Gulf Stream). The ridge and trough bottom irregularity off South Carolina known as the Charleston Bump causes a seasonal deflection of the Gulf Stream and resulting inshore southwest setting eddy currents occurring as far north as Cape Hatteras (Brooks and Bane 1978). These are effective around the 50-100 fathom curves and could be an important means of regional retention of eggs and larvae produced by *C. microps* and other shelf edge inhabitants.

Whether *C. microps* are strictly prematurationally or also functionally protogynous cannot as yet be confirmed. Winter (between spawning periods) collections are needed to determine whether transitional adults occur. The skewed sex ratios with size and age could indicate that sex reversal occurs over an extended range of ages rather than just prematurationally. However, skewed sex ratios with size could be attributable to differential growth rates, which have been noted for *C. microps* (Ross and Huntsman 1982) as well as *L. chameleonticeps* (Turner et al.[7]) and other tilefishes (Dooley 1978). Skewed sex ratios with age could result simply by <50% of the juvenile females changing sex to males. Furthermore, functional protogyny is questionable since 1) all males possessed solid testes, whereas secondary males generally retained remnants of the hollow ovarian lumen (Smith and Young 1966; Warner 1975a) and 2) the existence of 400-500 mm males would have entailed their sex reversal prior to functioning as reproductive females.

Prematurational sex reversal, evidenced by histological examination of juvenile gonads, accounts for the presence of oocytes in developing testes. The development of remnant ovarian gonocytes to previtellogenic oocytes in a testis could result from the activation of estrogens, the presence of which is implicit had there been a juvenile female stage (Bruslé 1969; Bruslé and Bruslé 1975). The males with residual oocytes were captured in the spring, the period of maximum hormonal induction for initiating gonadogenic activity (Hoar 1969). The residual oocytes were previtellogenic oocytes which 1) are reported to be the most resistant oocytes to resorption and atresia (Bruslé and Bruslé 1975) and 2) were observed in medial connective tissue or in collecting tubules and not interspersed within active spermatogenic tissue.

The occurrence of prematurational sex reversal in *C. microps* should indicate protogyny elsewhere in its genus or family. This is possible though not yet confirmed for several related species. Atlantic goldface tilefish, *C. chrysops*, captured off North Carolina and in the Gulf of Mexico ($n = 20$) include 7 females 385-

[7]Turner, S. C., C. B. Grimes, and K. W. Able. In prep. Age, growth mortality and age/size structure of the fisheries for tilefish, *Lopholatilus chameleonticeps*, in mid-Atlantic and southern New England waters. Department of Environmental Resources, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903.

503 mm TL and 13 males 503-562 mm TL (Ross unpubl. data). The sex ratio for anchor tilefish, *C. intermedius*, off Texas is 66 females:5 males between 100 and 270 mm TL, and 0 females:8 males >270 mm TL (Ross, Pavela, and Chittenden unpubl. data). Dooley (1978) reported anomalous sex ratios for *L. chameleonticeps*, *B. wardi*, and *B. serratus*. Clark and Ben-Tuvia (1973) reported pairs of *Malacanthus hoedtii* outside burrows including a large male and a smaller female. Prematurational sex reversal is also suspected of the tilefish, *L. chameleonticeps*, based on juvenile gonadal histology and adult sex ratio data (Grimes footnote 4).

Prematurational sex reversal in *C. microps* is likely a regression from monandric protogyny to functional gonochorism. The size-advantage model, which attributes protogyny to cases where an individual reproduces most efficiently as a female when young and a male when it gets older (Ghiselin 1969) is generally applicable when such things as inexperience, male dominance, mate selection, or territoriality lead to a differential in male reproductive success at older ages (Warner 1975b). Caulolatilids presumably evolved in the Caribbean and are often associated with reef-type habitat (Dooley 1978) where protogyny is widespread (Choat and Robertson 1975; Smith 1975; Warner 1975a, b). A radiation of *C. microps* (or ancestor) in the evolutionary past from a reef-type environment to more extensive outer continental shelf and upper slope habitats may have reduced the selection pressure favoring protogyny. The increase in utilizable habitat and more continuous distribution would allow more frequent opportunities for smaller males to engage in spawning, hence favoring sex reversal at an earlier age and ultimately tending toward secondary gonochorism.

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TEMPORAL AND SPATIAL PATTERNS OF NEARSHORE DISTRIBUTION AND ABUNDANCE OF THE PELAGIC FISHES OFF SAN ONOFRE-OCEANSIDE, CALIFORNIA

LARRY G. ALLEN[1] AND EDWARD E. DEMARTINI[2]

ABSTRACT

The pelagic fishes off San Onofre-Oceanside, California, were sampled nearshore (within 0.5-3.0 km of shore) during September 1979 to March 1981, using standardized lampara net gear. Sixty-two taxa were collected in 643 net-hauls systematically partitioned among three depth strata during day and night periods. *Engraulis mordax* dominated the catch and accounted for about 81% of all fishes. *Seriphus politus*, *Genyonemus lineatus*, *Peprilus simillimus*, and one species complex (atherinid spp.), together with *E. mordax*, made up >98% of the total numerical catch. Total catch per unit effort (CPUE) was greatest during the summer months (June-September), due mainly to the increased abundance of *Engraulis mordax*. The CPUE of other common species fluctuated little throughout the year except for a general decline during October-December because of the decreases in catches of *Seriphus politus* and *Genyonemus lineatus*. Four species groups were defined by quantitative clustering. Species Group I contained the above five most abundant and ubiquitous species. Groups II and III consisted of periodic species that occurred nearshore primarily during warmer and cooler water months, respectively. Group IV was composed of nine species of relatively rare bottom-oriented fishes.

The most conspicuous pattern exhibited by the common species in the assemblage involved a marked shift in depth over a diel period. *Engraulis mordax*, *Seriphus politus*, *Genyonemus lineatus*, and, to a lesser extent, *Peprilus simillimus* schooled in shallow water (5-11 m depths) during the day and dispersed offshore of these depths at night. Analysis of gut fullness during day and night suggested that *Seriphus politus*, and possibly *Genyonemus lineatus* and *Engraulis mordax*, disperse at night in part to feed on nocturnally active prey.

The marked depth and diel patterns of abundance that were observed could only be attributed in small part to depth-specific differences in water clarity and diel differences in catch efficiency.

Knowledge of pelagic fish assemblages that inhabit the waters off California is limited to general accounts from commercial catch records, larval fish studies and surveys (reviewed in Lasker 1982), and hydroacoustic surveys of adults (Mais 1974). These sources have provided general information on composition, distribution, and behavior of the offshore component of the pelagic ichthyofauna. This fauna is heavily dominated in numbers and biomass by the schooling clupeiform—northern anchovy, *Engraulis mordax*—especially within 37 km of the coast between Santa Barbara and San Diego (Mais 1974). Jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; Pacific sardine, *Sardinops sagax*; Pacific saury, *Cololabis saira*; and Pacific hake, *Merluccius productus*, are also important components of this fauna, although their relative abundances are poorly known (Mais 1974). Information on the relative abundances of pelagic fish stocks of nearshore (<3.0 km from shore) waters was limited to a few unpublished reports prior to the initiation of the present study.

Little is known about the diel and seasonal movements of fishes within the Southern California Bight, although the diel activity patterns of some fishes associated with kelp beds in the Bight have been documented (Ebeling and Bray 1976; Hobson and Chess 1976; Hobson et al. 1981). Several of these species (queenfish, *Seriphus politus*; salema, *Xenistius californiensis*; walleye surfperch, *Hyperprosopon argenteum*) are known to make diel migrations between kelp beds and nearshore pelagic and other coastal (e.g., sandy surf zone) habitats (Hobson and Chess 1976).

This study is the first direct, systematic assessment of the pelagic fish assemblage inhabiting nearshore (<3 km) waters off southern California. The specific purposes of this paper are to characterize this assemblage by 1) species composition, 2) major spatial and temporal patterns of abundance and distribution, 3) species associations, and 4) important environmental factors.

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METHODS

Field Sampling

Two longshore locations were sampled in the nearshore waters (0.5-3.0 km offshore) between San Onofre and Oceanside in southern California (Fig. 1). Fish abundances at these locations were monitored as part of an environmental impact assessment of the San Onofre Nuclear Generating Station (SONGS), located about 5 km downcoast of San Clemente, performed for the Marine Review Committee of the California Coastal Commission. The upcoast location is situated several kilometers downcoast of SONGS and the downcoast location ~18 km downcoast (Fig. 1). The sand and sand-cobble bottom in the area slopes gradually from shore with an increase in depth of about 5 m/km. The upcoast location is ~0.5-1.5 km downcoast of the San Onofre kelp bed (designated by stippling, Fig. 1).

Samples (net-hauls) were taken at randomly chosen positions within each of three depth blocks (shallow: 5-11 m; mid: 12-16 m; and deep: 18-27 m) at both locations during day (1-6 h after dawn) and night (1-6 h after sunset) periods from September 1979 to March 1981, inclusive. (Samples could not be taken in January-February 1980, when our sampling vessel was drydocked for repairs.) The three depth blocks used were chosen as most appropriate for partitioning onshore/offshore variation in catches, based on the results of prior (May 1978-August 1979) lampara sampling at various depths in the general area. The number of cruises ($N = 1$-4) and net-hauls ($N = 4$-8) per month differed between diel periods and depth blocks, with most samples allocated to the daytime period and shallow depth block wherein catches were most variable. Because we suspected a significant date (cruise) effect on our catches, a paired sampling design was established in which the same depth blocks were sampled during the same diel period at both longshore locations on each cruise.

Two sizes of lampara net (semipursing round haul, Scofield 1951) were used: 1) A small net with each of two wings 118 m long of 15 cm stretch mesh, tapering to a bag of 1.25 cm mesh, was used to sample surface-to-bottom within the 5-11 m and 12-16 m depth blocks. The small net sampled about 4,600 m^2 of sea surface area. 2) A large net with wings each 136 m long of mesh identical to the small net was used to sample the 18-27 m depth block, wherein it also fished surface-to-bottom. The large net sampled about 6,200 m^2 of sea surface area. Catch was standardized to the area of the small lampara net. Both nets took about 10 min to set and retrieve, using a commercial fishing vessel. The same vessel and procedures of net deployment were used for the duration of the study.

Fishes collected in net-hauls were transferred by dip net to a holding tank on the vessel and were then identified and counted. Subsamples of major species were taken for life history analysis, and other fishes were returned to the sea as soon as possible. Large catches were subsampled with standard bait brailers.

In order to evaluate the potential effects of variable net catch efficiencies under varying water clarity conditions during the day, an index of water clarity (visibility to shipboard observer of 30 cm Secchi disk) was measured immediately following most net-hauls. Potential diel differences in catch efficiency were evaluated on the basis of the percentage recapture of marked *Seriphus politus* in net-hauls made during a pilot (June-September 1978) study. A constant number (50) of fin-clipped adult *S. politus*, captured on the previous net-haul, were released within the center of the area being encircled as the net was deployed. Test releases were made in all depth blocks, both at the surface and near bottom (via a messenger-tripped holding cage), and during both day and night. Secchi disk indices of water clarity were measured at night between test net-hauls, using a standard shipboard light source.

Data Analysis

Analyses were carried out using the Statistical Analysis System (SAS) installed at the Marine Review Committee's Computer Center in Solana Beach, Calif.

Preliminary tests (*t*-test for paired comparisons, $P > 0.05$) failed to detect significant differences between locations in all but a few of the common species using log-transformed catch data. Log transformation ($\log_{10} X + 1$) of catch data was necessary to satisfy the parametric assumptions of normality and equality of variances within depth blocks and diel periods. The general lack of longshore differences allowed us to pool the data at both locations for subsequent analyses.

Catch per unit effort (CPUE) was calculated by month based on log-transformed catch data for individual depth blocks and diel periods. Combined CPUE of all three depth blocks was expressed as the grand mean and associated standard error of depth means.

Comparisons of untransformed catch data between depths, diel periods, and dates were made by using Wilson's nonparametric analysis of variance (Wilson

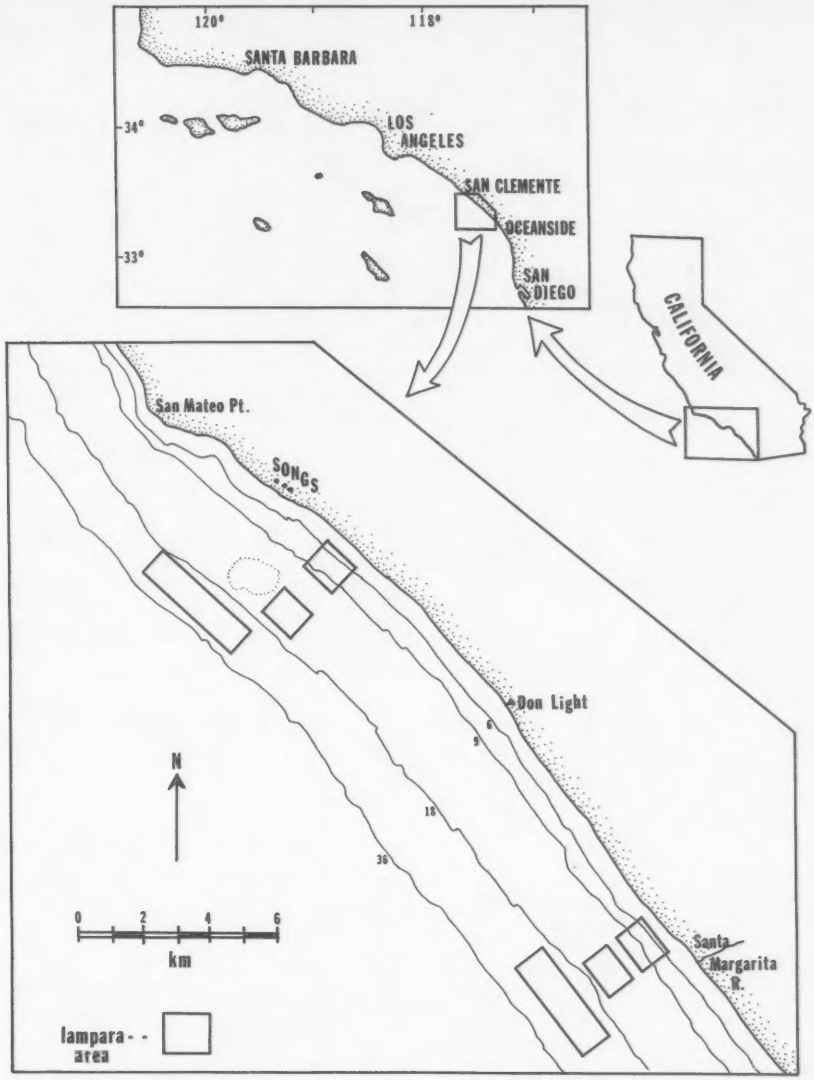

FIGURE 1.—Map of the study area, San Onofre-Oceanside, Calif. Rectangles represent the various depth blocks sampled at the two longshore locations; note that all depth blocks are 1 km distance in onshore-offshore extent. Stippled area represents the location of the San Onofre kelp bed.

1956), available in the IMSL Library's[3] statistical package. Variances of catches were heteroscedastic among depth blocks and between diel periods, which precluded use of parametric analysis of variance. Wilson's three-way ANOVA's (either with unequal replication or without replication) were used, depending on the category (e.g., total individuals or species counts) or species being considered.

Quantitative clustering of species was carried out using the Ecological Analysis Package (EAP)[4]. Mean abundance of species by cruise date, depth, and diel period was transformed by its square-root in order to counter the tendency of the Bray-Curtis Index (Clifford and Stephenson 1975) to overemphasize abundant species. Flexible sorting was used to maximize the separation between groups. Only species with a minimum total occurrence of 20 were considered in this analysis.

Spearman's rank correlations (r_s) were calculated to examine the relationships between diel period, water depth, and surface water temperature and CPUE for 1) total individuals, 2) total individuals minus *E. mordax*, 3) certain major species, and 4) species counts. CPUE data for taxonomic categories 1-3 were related to water clarity by using Spearman's rank test within each depth block; in addition, a parametric analysis of covariance (ANCOVA), with water clarity as covariate of CPUE and depth block as the treatment effect, was performed to estimate the general magnitude of the potential influence of depth-specific differences in water clarity on daytime catches. Diel catch efficiency data for *Seriphus politus* were related to water clarity by parametric or Spearman rank correlation, as appropriate.

Day-Night Comparison of Foregut Fullness

Preliminary examination of the variance: mean ratios of CPUE data indicated that fishes were dispersed more at night than during the day. In order to investigate the possible role of feeding behavior in this nocturnal dispersal pattern, we examined archived stomachs from paired day (1000-1300 h) and night (2100-0100 h) samples of fishes of comparable sizes for the five most abundant taxa (*E. mordax*; *Seriphus politus*; white croaker, *Genyonemus lineatus*; Pacific butterfish, *Peprilus simillimus*; and atherinid spp., the latter represented by jacksmelt, *Atherinopsis californiensis*). Contents of the foregut were removed, either dried at 40°C (for *E. mordax*, *S. politus*, and *G. lineatus*) or blotted dry (*P. simillimus* and *A. californiensis*), and weighed. A contents index (CI) was then calculated for each specimen as follows:

$$CI = (\text{weight contents}/\text{weight of fish}) \times 10^5.$$

Diel overlap in gut evacuation did not create a major problem except that it tended to make the analysis more conservative (i.e., more difficult to detect day-night differences).

The CI's for day-caught versus night-caught fishes were compared by either Wilcoxon signed-ranks test for paired comparisons or Wilcoxon two sample test, depending on the number and temporal distribution of samples.

RESULTS

Species Composition

Sixty-two taxa representing 33 families of teleost and elasmobranch fishes were collected in 643 net-hauls partitioned among the three depth blocks and two diel periods made during the 19-mo period, September 1979-March 1981 (Table 1). The catch was overwhelmingly dominated by *E. mordax*. *Seriphus politus*, *G. lineatus*, *P. simillimus*, and a species complex of silversides (atherinid spp.) were also abundant in the catch. These top five taxa accounted for >98% of the numbers of total individuals sampled (Table 1). The atherinid species complex was a composite of three species (*Atherinopsis californiensis*; topsmelt, *Atherinops affinis*; California grunion, *Leuresthes tenuis*) that were not readily identifiable in the field. Subsamples of "atherinid spp." field catches were about 48% *Atherinopsis californiensis*, 42% *L. tenuis*, and 10% *Atherinops affinis*.

Location Comparison

Location differences were insignificant ($P > 0.05$) for most categories and species within depth blocks and diel periods based on *t*-tests for paired comparisons. Differences were detected in the following cases: 1) Atherinids were more abundant at night in the upcoast area ($P < 0.01$); 2) Pacific barracuda, *Sphyraena argentea*, occurred in greater numbers at night upcoast ($P < 0.01$); 3) *T. symmetricus* was more abundant both day and night upcoast ($P < 0.01$); and 4) *Scomber japonicus* was also caught in greater numbers upcoast ($P < 0.05$), but only at night during the

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period November 1980-March 1981. *Xenistius californiensis* was consistently more common upcoast ($N = 170$ sample fish) than downcoast ($N = 13$) at night, although its low frequency of overall occurrence precluded a statistical test for longshore differences.

TABLE 1.—Number of individuals and frequency of occurrence of 62 species/taxa in 643 lampara net samples on 129 cruises from September 1979 to March 1981, inclusive. Species/taxa are ranked according to total number of individuals.

Species/taxa	Number	Percent number	Frequency	Percent frequency
Engraulis mordax	819,872	80.79	440	68.4
Seriphus politus	80,513	7.93	413	64.2
Genyonemus lineatus	53,994	5.32	335	52.1
Peprilus simillimus	26,003	2.56	238	37.0
Atherinid spp.	15,811	1.56	326	50.7
Scomber japonicus	7,386	0.73	194	30.2
Trachurus symmetricus	2,750	0.27	92	14.3
Anchoa compressa	1,915	0.19	85	13.2
Sarda chiliensis	1,394	0.14	115	17.9
Sphyraena argentea	1,066	0.11	99	15.4
Hyperprosopon argenteum	936	0.09	106	16.5
Phanerodon furcatus	665	0.07	101	15.7
Myliobatis californica	455	0.04	212	33.0
Menticirrhus undulatus	412	0.04	117	18.2
Umbrina roncador	269	0.03	38	5.9
Amphistichus argenteus	211	0.02	51	7.9
Xenistius californiensis	182	0.02	25	3.9
Paralichthys californicus	139	0.01	79	12.3
Sardinops sagax	130	0.01	15	2.3
Paralabrax nebulifer	108	0.01	56	8.7
Cymatogaster aggregata	86	0.01	34	5.3
Squalus acanthias	66	0.01	23	3.6
Scorpaena guttata	57	0.01	28	4.3
Urolophus halleri	34	<0.01	19	2.9
Citharichthys stigmaeus	28	<0.01	16	2.5
Otophidium scrippsi	27	<0.01	19	2.9
Rhinobatos productus	22	<0.01	12	1.9
Platyrhinoidis triseriata	21	<0.01	18	2.8
Anisotremus davidsoni	19	<0.01	8	1.2
Medialuna californiensis	19	<0.01	5	0.8
Torpedo californica	18	<0.01	15	2.3
Cynoscion nobilis	17	<0.01	12	1.9
Pleuronichthys verticalis	12	<0.01	13	2.0
Raja inornata	12	<0.01	8	1.2
Rhacochilus toxotes	11	<0.01	4	0.6
Porichthys myriaster	9	<0.01	5	0.8
Porichthys notatus	8	<0.01	4	0.6
Alopias vulpinus	8	<0.01	5	0.8
Pleuronichthys ritteri	8	<0.01	5	0.8
Embiotoca jacksoni	8	<0.01	6	0.9
Sebastes auriculatus	7	<0.01	1	0.1
Roncador stearnsi	6	<0.01	2	0.3
Hypsopsetta guttulata	6	<0.01	5	0.8
Dorosoma petenense	4	<0.01	4	0.6
Paralabrax clathratus	4	<0.01	4	0.6
Damalichthys vacca	4	<0.01	1	0.1
Leptocottus armatus	4	<0.01	3	0.5
Syngnathus spp.	4	<0.01	4	0.6
Citharichthys xanthostigma	3	<0.01	3	0.5
Triakis semifasciata	3	<0.01	3	0.5
Raja binoculata	2	<0.01	1	0.1
Xystreurys liolepis	2	<0.01	2	0.3
Heterostichus rostratus	2	<0.01	2	0.3
Cypselurus californicus	2	<0.01	2	0.3
Heterodontus francisci	1	<0.01	1	0.1
Sebastes rastrelliger	1	<0.01	1	0.1
Balistes polylepis	1	<0.01	1	0.1
Synodus lucioceps	1	<0.01	1	0.1
Symphurus atricauda	1	<0.01	1	0.1
Mugil cephalus	1	<0.01	1	0.1
Icichthys lockingtoni	1	<0.01	1	0.1
Mustelus californicus	1	<0.01	1	0.1
Grand total	1,014,762		643	

Monthly and Longer Temporal Patterns

CPUE for total individuals, number of *E. mordax*, and total individuals minus *E. mordax*, when plotted on a monthly basis, revealed general temporal patterns of abundance (Fig. 2). Catches were generally higher at night for all three categories (see below). Day catches were generally much more variable than night catches, as the standard errors indicate (Fig. 2). The longer term (i.e., "seasonal") temporal changes in the catch of total individuals largely reflect the increase in primarily juvenile-sized (<10 cm standard length, Hunter and Leong 1981) *E. mordax* during the summer months. When the abundances of all species other than *E. mordax* are combined, the catch remained relatively constant throughout the study period except for a general decline in numbers during October-December of both 1979 and 1980.

The abundances of *Seriphus politus* and *G. lineatus* also remained relatively constant except for the October-December declines. These two species (Fig. 3) were primarily responsible for the pattern observed for total individuals minus *E. mordax*. Night catches were higher than day catches for *G. lineatus* and (especially) *S. politus*. The abundances of *P. simillimus* and atherinids in general showed patterns which were similar in terms of seasonality. Both were usually more abundant during cooler water months (December-April). Three species of higher level (mainly piscivorous) carnivores showed dissimilar patterns of nearshore abundance (Fig. 3). *Scomber japonicus* was more abundant in warmer water months from about June to October. Pacific bonito, *Sarda chiliensis*, occurred in greatest numbers from March to August, but only during the day. *Sphyraena argentea* was more abundant during the cooler water months of October through March.

Diel and Depth Patterns

Day and night catches of total individuals varied among depth blocks throughout the study (Fig. 4). Day catches were consistently highest at 5-11 m depths, but the variability in catches was high. Night catches did not differ ($P > 0.05$, Wilcoxon's signed rank test) from day catches in the shallow depth block. However, night catches were higher and less variable than day catches in both the 12-16 m and 18-27 m depth blocks (Fig. 4).

All categories and species common enough to test showed significant diel, depth, and date (cruise) main effects, as well as diel × depth interactions, based on Wilson's three-way ANOVA with unequal replication

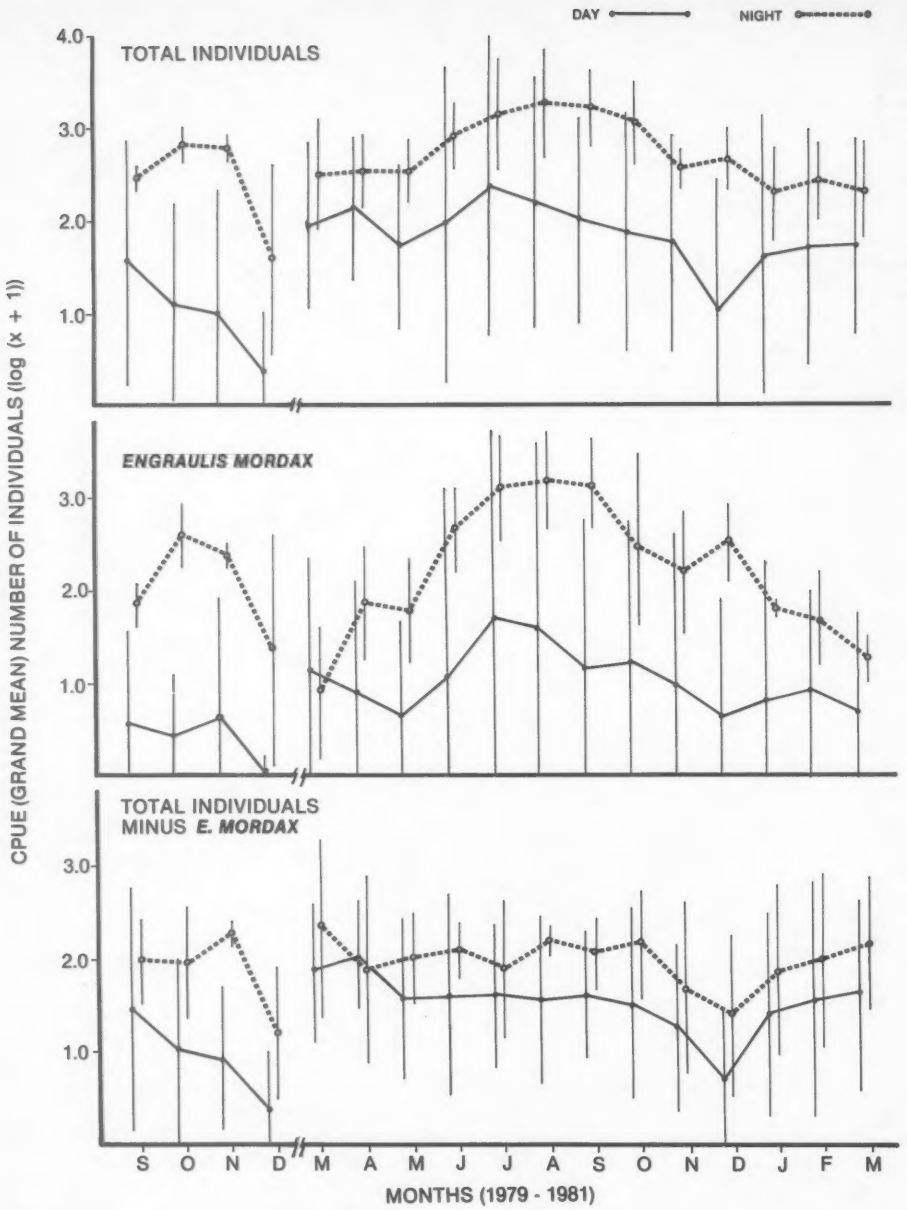


FIGURE 2.—Monthly variation in the abundance (CPUE) of total individual fishes, *Engraulis mordax*, and total individuals minus *E. mordax* over the study period. Each value represents the grand mean of $\log_{10}(X+1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

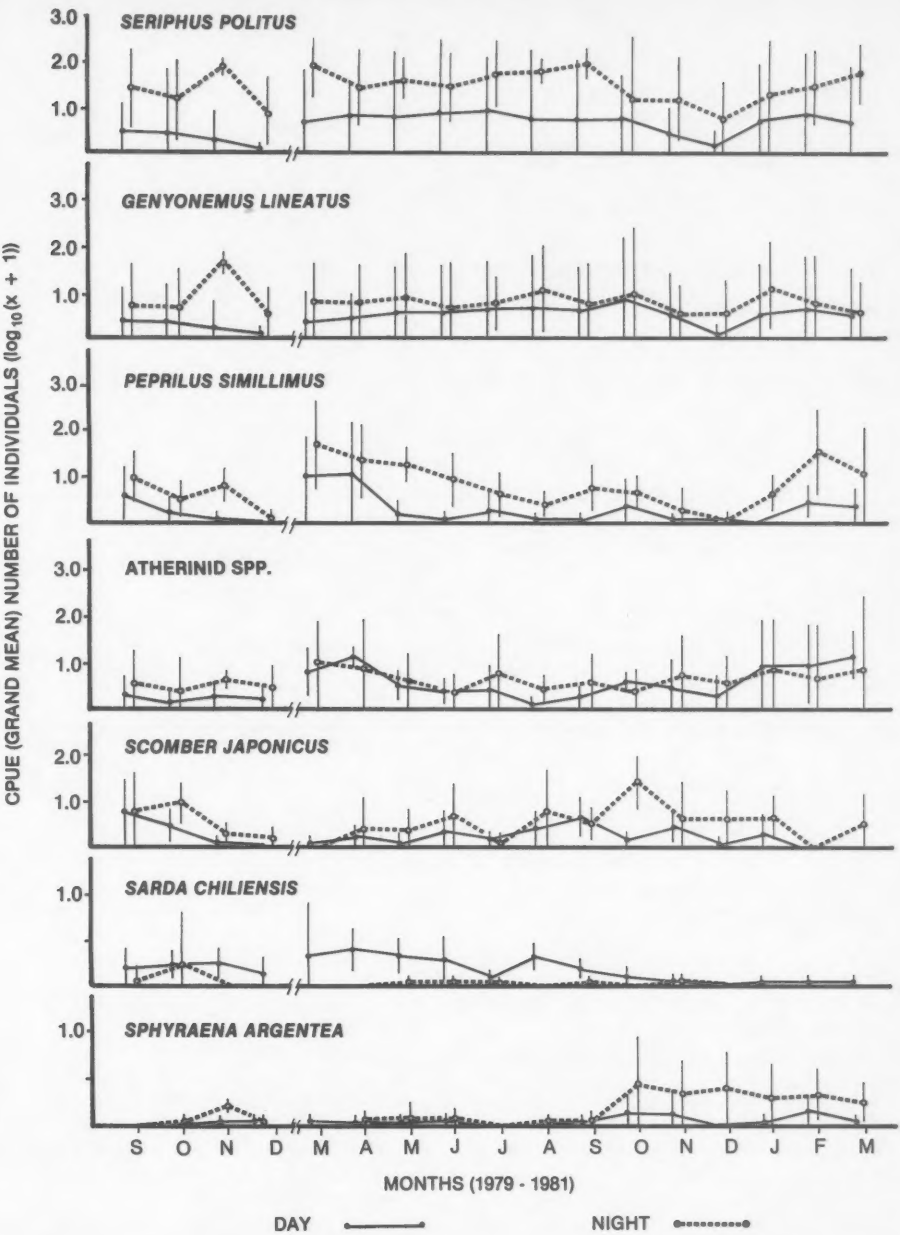


FIGURE 3.—Monthly variation in day and night catches of seven common species and one taxon of fishes over the study period. Each value represents the grand mean of $\log_{10}(X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

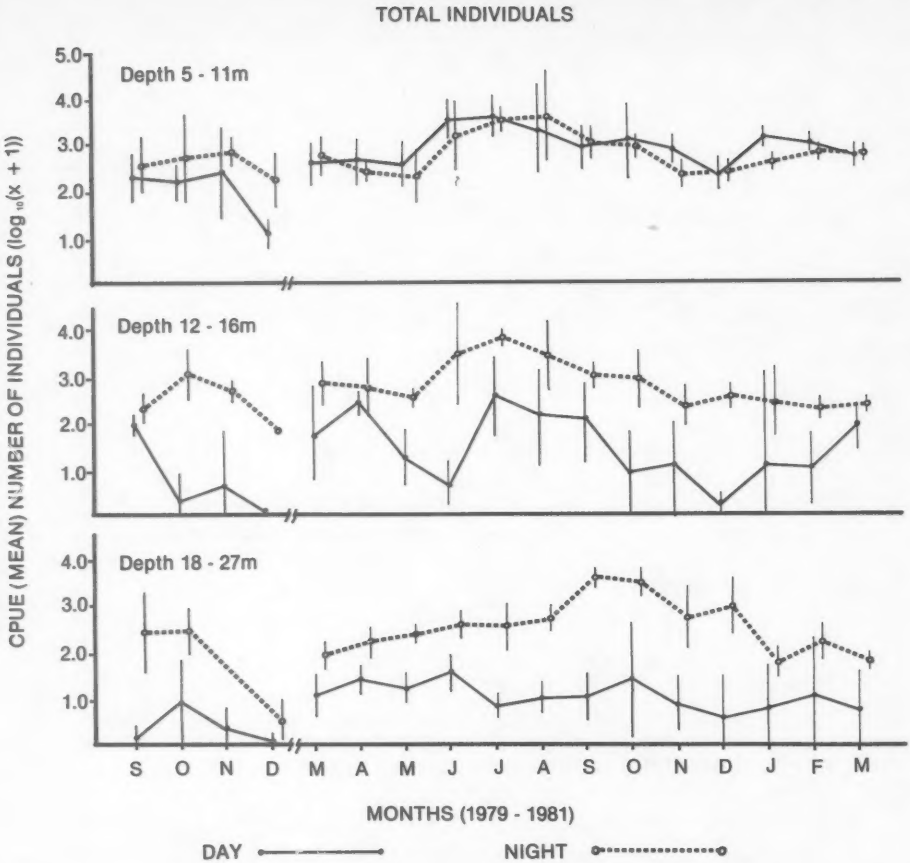


FIGURE 4.—Monthly variation in the total number of individual fishes captured during the day and night in each of three depth blocks over the study period. Each value represents the grand mean of $\log_{10}(X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

(Table 2). The probability for a date effect on *E. mordax* was marginal at $P = 0.09$.

Diel, depth, and date effects were variously important for four other common taxa or categories (Table 3). Interactions between main effects could not be evaluated for these species because we were forced to use Wilson's ANOVA without replication in order to minimize the number of zeros in the catch data. *Peprilus simillimus* was more abundant at night (diel effect) and on certain cruises during the study period (date effect). Catches of *G. lineatus* were higher at night and at the shallow depth. *Scomber japonicus* was more abundant offshore and at certain times of year.

Species Associations

Quantitative clustering of species by sample abundance among depth blocks and diel periods produced four distinct groups within 21 species (Fig. 5). The largest dichotomy (~160% distance) occurred between members of Groups I-II and Groups III-IV. Separation within both Groups I-II and Groups III-IV occurred at ~65% distance.

In Group I *E. mordax* was most dissimilar, fusing with other group members at ~55% distance. *Seriphus politus* and *G. lineatus* formed a very close association, being linked at ~12% distance. *Peprilus*

TABLE 2.—Summary of significant chi-square values from Wilson's three-way ANOVA with unequal replication for three categories and two species of fishes present in lampara net samples, September 1979-March 1981, inclusive (*=P<0.001). Dashes indicate insignificant (P <0.05) results.

Category or species	Diel	Depth	Date	Diel × depth	Diel × date	Depth × date	D × D × D
Total individuals	42.7**	58.9**	22.6*	29.3**	—	—	—
Total individuals minus *Engraulis mordax*	8.1*	87.4**	24.9*	10.6*	—	—	—
Species counts	26.2**	90.9**	26.8*	22.4**	—	—	—
Engraulis mordax	82.4**	22.2**	—	37.7*	—	—	—
Seriphus politus	63.4**	79.4**	26.0*	32.6*	—	—	—
df	1	2	13	2	13	26	26

TABLE 3.—Results of Wilson's three-way ANOVA without replication for four species that were common in lampara net samples, September 1979-March 1981, inclusive. (* = $P \leq 0.05$; ** = $P \leq 0.001$.)

Factor	X^2	df	P
Peprilus simillimus			
Diel	17.30	1	<0.001**
Depth	1.15	2	0.563
Date	24.36	13	0.028*
Genyonemus lineatus			
Diel	4.76	1	0.029*
Depth	48.29	2	<0.001**
Date	8.00	13	0.844
Atherinid spp.			
Diel	0.05	1	0.827
Depth	27.86	2	<0.001*
Date	13.64	13	0.400
Scomber japonicus			
Diel	2.34	1	0.126
Depth	8.90	2	0.012*
Date	25.70	13	0.019*

simillimus and atherinid spp. also formed a close association (~18% distance).

Sarda chiliensis was the most dissimilar member of Group II, and linked to *Scomber japonicus* and *T. symmetricus* at ~40% distance.

The four species in Group III formed a relatively tight group with a maximum dissimilarity of only 38% distance (yellowfin croaker, *Umbrina roncador*, to the other three species). *Sphyraena argentea* and *X. californiensis* were most closely associated (~20% distance), with deepbody anchovy, *Anchoa compressa*, occupying the intermediate position.

Group IV was composed of nine bottom-oriented species which were relatively rare in the samples.

Influences of Diel Period, Surface Water Temperature, and Depth

Sea surface temperature ranged from about 14.2° to 24.0°C during the study period. Highest water temperatures were encountered during the summer months (July-September) and lowest in winter (December-February) as would be expected in a temperate marine habitat. Sampling depths ranged from 5 to 25 m. Day collections were made between 0700 and 1300 h and night collections between 1900 and 0100 h.

Spearman rank correlations of 2 categories and 21 individual species (Table 4) with time of collection, depth of water column, and sea surface temperature yielded numerous significant relationships. Depth (20 significant values) and time of collection (14) were important factors for most categories or species. Temperature was significantly correlated with 10 categories or species. The total individuals category was significantly correlated with all three abiotic factors (negative with depth). Species counts correlated only with depth (negative) and time of collection. In general, both the numbers of individuals and numbers of species were greatest at

TABLE 4.—Summary of Spearman's rank correlation (r_s) values and significance levels for 2 categories and the 21 abundant species/taxon collected. Time = time of collection (military time); Depth = bottom depth (m); Temp = surface water temperature (°C). (df = 210; * = $P \leq 0.05$; ** = $P \leq 0.0001$.)

Category or species/taxon	Environmental variables			Species group
	Time	Depth	Temp.	
Total individuals	0.44**	−0.46**	0.22*	—
Species counts	0.43**	−0.62**	0.11	—
Engraulis mordax	0.48**	−0.33**	0.22*	I
Seriphus politus	0.46**	−0.56**	0.11	I
Genyonemus lineatus	0.31**	−0.71**	0.08	I
Peprilus simillimus	0.54**	−0.21*	0.04	I
Atherinid spp.	0.16*	−0.52**	−0.22*	I
Scomber japonicus	0.12	0.28**	0.40**	II
Trachurus symmetricus	0.15*	0.25**	0.08	II
Sarda chiliensis	−0.27**	0.05	0.27**	II
Anchoa compressa	−0.01	−0.52**	−0.14*	III
Sphyraena argentea	0.20*	−0.25**	−0.14*	III
Umbrina roncador	0.11	−0.32**	−0.14*	III
Xenistius californiensis	0.12	−0.14*	−0.06	III
Myliobatis californicus	0.04	−0.22**	0.26**	IV
Phanerodon furcatus	0.14*	−0.46**	−0.02	IV
Hyperprosopon argenteum	0.05	−0.54**	−0.01	IV
Menticirrhus undulatus	−0.09	−0.60**	0.06	IV
Amphisticus argenteus	−0.17*	−0.45**	0.01	IV
Cymatogaster aggregata	0.14*	−0.35**	0.07	IV
Paralichthys californicus	0.07	−0.48**	0.01	IV
Paralabrax nebulifer	−0.03	0.01	0.22**	IV
Scorpaena guttata	0.27**	−0.11	0.02	IV

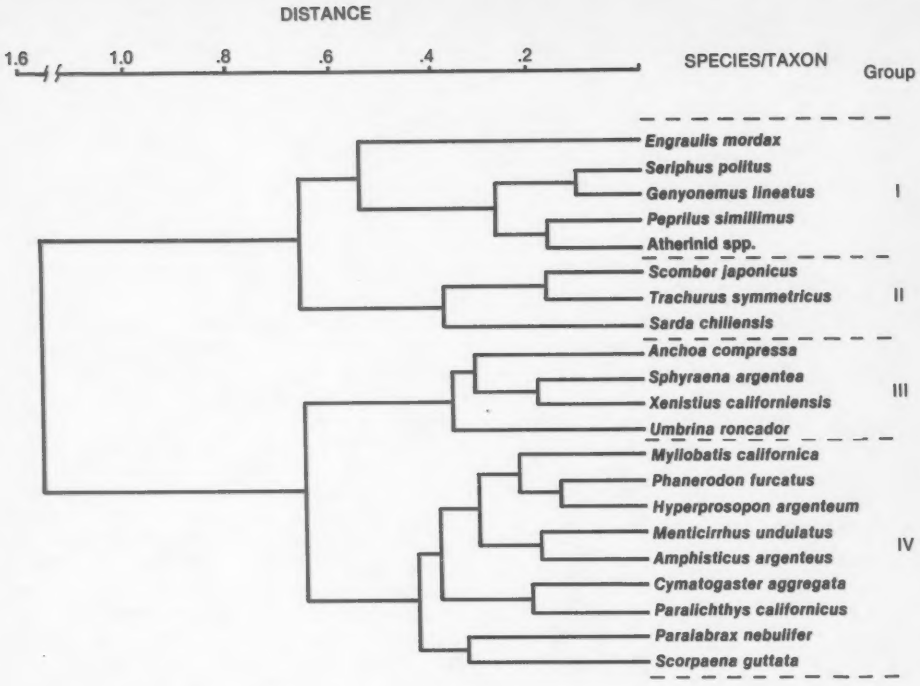


FIGURE 5.—Dendrogram depicting the clustering of 20 species and 1 taxon based on abundance within lampara samples. Four species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (ecological distance).

shallow depths during the night. More individuals were collected during the warmer months, although this relationship was highly dependent on the catches of *E. mordax*.

The catches of all the members of species Group I were correlated with time of collection and depth (negative) (Table 4). Only the abundances of *E. mordax* (positive) and atherinid spp. (negative) were correlated with temperature. *Scomber japonicus* and *T. symmetricus* of Group II were usually found farther offshore in the study area (positive with depth). The catches of *S. japonicus* and *Sarda chiliensis* were positively correlated with temperature. However, *T. symmetricus*, like many of the other species, was collected in greater numbers at night, while *S. chiliensis* was captured almost exclusively during the day. The catches of all members of species Group III were negatively correlated with depth and temperature, although the temperature correlation for *X. californiensis* was not significant. Six of the eight species in species Group IV were negatively correlated with depth, although no other consistent pattern was apparent.

The occurrence and distribution of the 21 abundant species are displayed graphically in relation to diel period and depth in Figures 6 and 7. Species are presented in the species groups derived for the dendrogram of species associations (Fig. 5). Only species with >10% occurrence during the particular diel period are included in the illustrations.

During daylight periods, species Groups I, III, and IV were distributed close to shore, mostly within the 5-11 m depth block (Fig. 6). The high variance of catches during the day indicated that the species are highly clumped in distribution and are probably schooling at this time (especially members of Groups I and III). Species of Group II were primarily found offshore within the 12-16 m and 18-27 m depth blocks and occurred mainly during the warmer months. Group III on the other hand occurred during the colder months.

At night the distribution of species was quite dif-

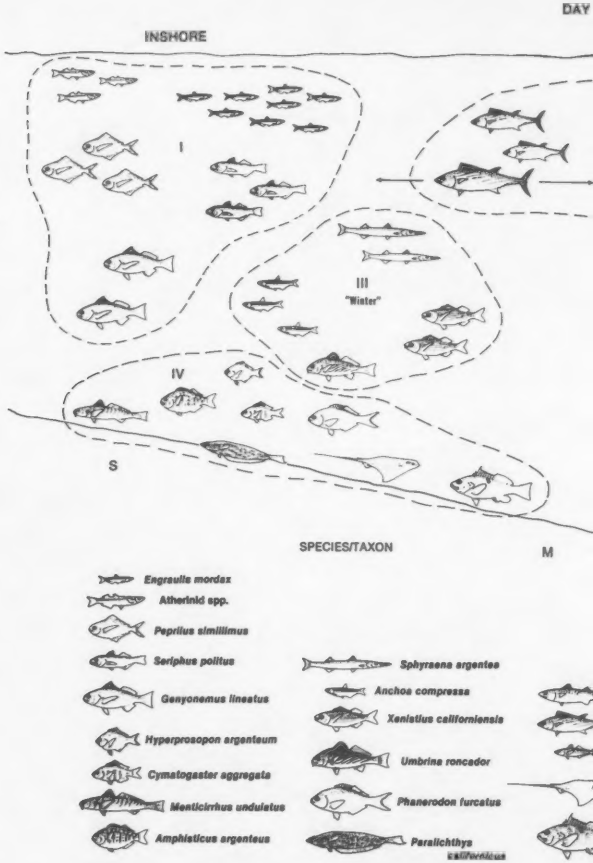


FIGURE 6.—Generalized illustration of the principal fish species (and taxon) present in t
lines enclose species groups derived from the Figure 5 dendrogram. Inclusion of species
movement. Fishes are not drawn strictly to scale. S, M, and D represent shallow, midd

ent in the nearshore waters off San Onofre-Oceanside, Calif., during daylight hours. Dashed
species is limited to those that were caught on >20 cruises. Arrows indicate onshore-offshore
, middepth, and deep blocks, respectively.

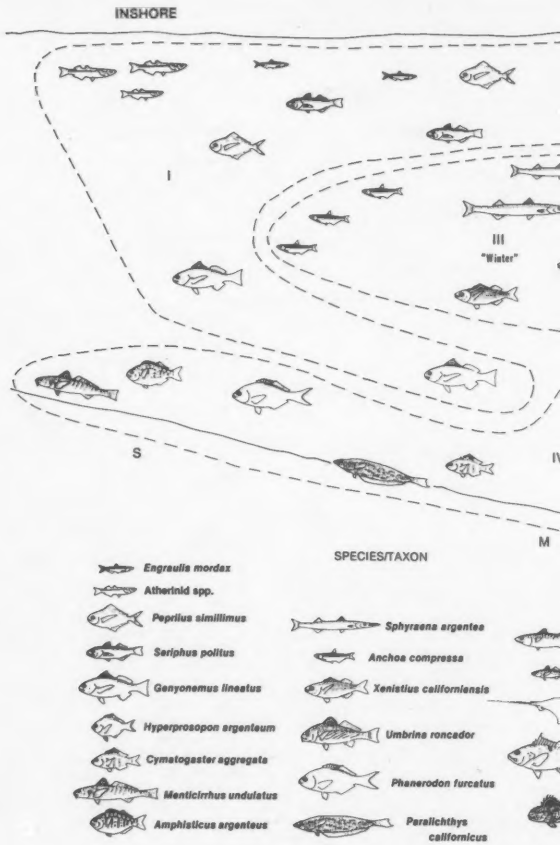
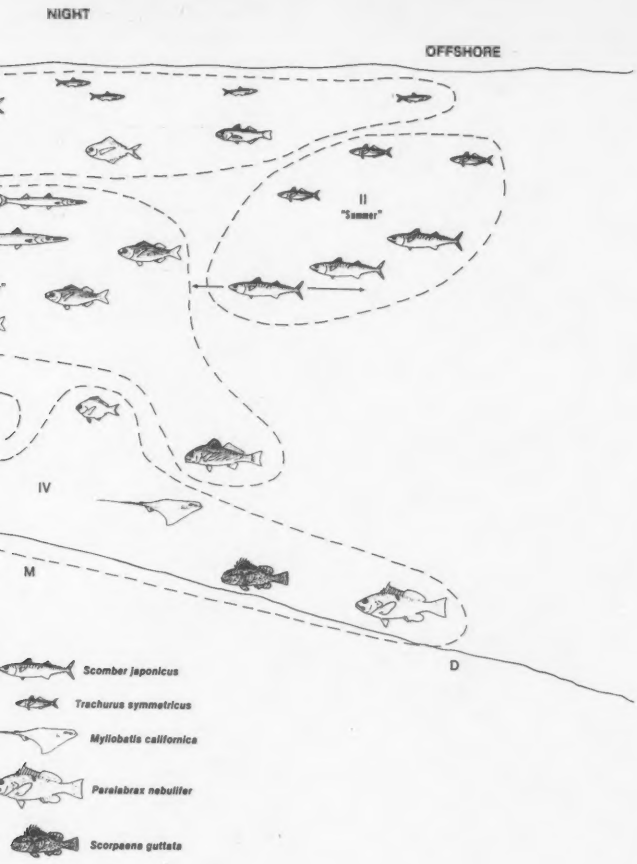


FIGURE 7.—Generalized illustration of the principal fish species (and taxon) present



resent in the nearshore waters off San Onofre-Oceanside, Calif., at night. Other information as in Figure 6.

ferent (Fig. 7). Members of Group I (especially *E. mordax*, *Seriphus politus*, and *G. lineatus*) dispersed offshore, resulting in a much more even distribution of individuals among net-hauls. Certain species in Groups III and IV also moved offshore at night. Group II persisted over the deeper portions of the study area, with *Sarda chiliensis* absent at night.

Interrelations of Depth Block, Water Clarity, and CPUE

The relations between CPUE and water clarity were significantly negative for five of seven major taxa in one or more depth blocks during the day (Table 5). Water clarity differed significantly among depths (Shallow block: $\bar{x} = 4.4$ m; middepth block: 6.8 m; deep block: 9.6 m; Kruskall-Wallis $H = 33.8$, $df = 2$, $P < 0.001$). ANCOVA results, however, indicated that, although water clarity in addition to depth block were in general negatively related to daytime catches, there were no depth by water clarity interactions (all $P > 0.10$). On average, only an estimated 12-16% of the total variation in the CPUE of major taxa was attributable to variations in water clarity with any depth block (Table 5).

Diel Effects on Catch Efficiency

The percentage recapture of fin-clipped *Seriphus politus* on average was significantly ($P < 0.05$) greater ($\bar{x} \pm SE = 13 \pm 3\%$, $N = 40$ net-hauls) during the day versus night ($25 \pm 3\%$, $N = 24$ hauls). Parametric estimators for the percentage recapture versus water clarity relation were not possible for daytime tests due to the nonnormality of these data; however, about 30% of the variation in the ranks of daytime recapture data was attributable to water clarity ($r_s = -0.54$, $P < 0.001$). Queenfish recaptures at night were insignificantly (Pearson's $r = -0.31$, $P = 0.14$) related to water clarity.

Day-Night Feeding Comparison

No significant differences in stomach fullness (CI) were found between day- and night-caught specimens of *E. mordax*, *G. lineatus*, and *P. simillimus* (Table 6). Specimens of *Seriphus politus*, however, had significantly greater foregut fullness at night, while those of *Atherinopsis californiensis* had significantly greater fullness during the day (Table 6).

TABLE 5.—Summary of Spearman's rank correlation (r_s) values and significance levels for comparisons of CPUE and water clarity within depth blocks for two categories and four major species plus one taxon (* = $P < 0.05$; ** = $P < 0.001$). Dashes indicate insignificant ($P > 0.05$) results. Also indicated is the estimated percentage of total variation (R^2) of daytime CPUE explained by variation in water clarity in each depth block. R^2 approximations reflect results of parametric regressions performed in an ANCOVA with water clarity as covariate and depth block as treatment.

Category or species/taxon	Rank correlation (Spearman's r_s)			Estimated % variance (= R^2)		
	5-11 m	12-16 m	18-27 m	5-11 m	12-16 m	18-27 m
Total individuals	−0.36*	−0.61**	—	20	37	24
Total individuals minus *Engraulis mordax*	—	−0.58**	−0.60*	13	32	33
Engraulis mordax	—	−0.34*	—	15	11	8
Seriphus politus	−0.31*	−0.34*	—	18	9	9
Genyonemus lineatus	—	—	—	8	2	—
Peprilus simillimus	—	—	—	6	7	6
Atherinid spp.	—	−0.45*	—	3	17	12

TABLE 6.—Summary of results of day versus night comparisons of the contents index (CI) of foregut samples of the five most abundant fishes present in lampara collections (* denotes statistical significance).

TEST—Wilcoxon signed-rank test of median CI for paired day-night samples

Species	N (day-night)	Paired N	Ts	P	
Engraulis mordax	40/36	8	14	0.29	NS
Seriphus politus	49/49	9	4	0.02	(night>day)*
Genyonemus lineatus	42/44	9	18	0.30	NS

TEST—Wilcoxon two-sample test

Species	N (day-night)	Z	P	
Peprilus simillimus	26/16	0.13	0.90	NS
Atherinopsis californiensis	29/33	5.42	<0.001	(day>night)*

DISCUSSION

The nearshore pelagic ichthyofauna between San Onofre and Oceanside, Calif., was dominated by silvery-sided, schooling fishes. *Engraulis mordax*, the dominant pelagic species offshore (Mais 1974), was also the most abundant species nearshore. *Seriphus politus* and *G. lineatus*, the two abundant sciaenids in this assemblage, are best characterized as bottom associated fishes which rise into the water column. Both of these species are well represented in bottom-trawls in the area.[5] *Genyonemus lineatus* is generally more abundant in trawls, indicating that it is more closely associated with the bottom than *S. politus*. The three species above, together with *P. simillimus* and atherinid spp., constituted species Group I. Members of this group were abundant and ubiquitous within the area and accounted for >98% of the total individuals collected. Species Groups II and III represented periodic components (Tyler 1971) within the assemblage. Group II comprised three species of higher carnivores that generally occurred in the offshore portion of the study area during the warmer months (spring-summer). Group III, on the other hand, contained four species that were more abundant at shallow depths during the colder water months (fall-winter). Two of these species, *Anchoa compressa* and the sciaenid *Umbrina roncador*, are known to occur in bay-estuarine habitats such as Newport Bay during the summer months (Horn and Allen 1981). Both *A. compressa* and *U. roncador* belong to primarily tropical families. The presence of these two species in the study area during fall-winter suggests that they may seasonally migrate out of embayments and into shallow coastal waters in response to cool-water temperatures. The bottom-associated species of Group IV were relatively rare in catches with the exception of the bat ray, *Myliobatis californica* (California bat ray). *Myliobatis californica* occurred in about one-third of all net-hauls and ranked sixth in number of total occurrences. Its relatively large size ($\tilde{x} \simeq 2$ kg) and high frequency of occurrence make *M. californica* a more important component of this nearshore assemblage than numerical abundance alone would indicate.

Upcoast and downcoast locations were generally similar in terms of total individuals, species counts, and in the abundances of most common species. The few exceptions (atherinids, *Sphyraena argentea*, *Trachurus symmetricus*, *Xenistius californiensis*) that were more abundant at the upcoast location probably reflect the proximity of the San Onofre kelp bed. All of these species are known to associate with kelp beds or rocky reefs at some time during the year (Feder et al. 1974; Hobson and Chess 1976; Mais 1974).

Significant date effects found by Wilson's ANOVA's reflected a certain amount of temporal variation within this assemblage of fishes. Some of these date effects can be attributed to spatial patchiness and sampling error; other date effects undoubtedly reflect short-term, temporal changes in the environment. Upwelling is probably a major factor contributing to short-term variation in the abundance and distribution of these fishes. The waters within the Southern California Bight can be subjected to bouts of upwelling anytime during the year, although upwelling is most likely to occur during March-July (Parrish et al. 1981). Both short-term temperature variations due to upwelling and long-term seasonal warming and cooling of coastal waters probably influenced the 10 observed correlations between sea surface temperature and the abundance of individual taxa. The abundances of only two of the top five taxa however were significantly correlated to sea temperature (*Engraulis mordax*, positive; atherinids, negative). *Peprilus simillimus*, the fourth most abundant species, varied significantly between dates (ANOVA results), but showed no significant relationship to temperature. Extremely patchy distributions and high vagility might account for the observed short-term variations in the abundance of *P. simillimus*. Neither *Seriphus politus* nor *Genyonemus lineatus* varied greatly in seasonal abundance although *S. politus* did show a significant date effect (ANOVA) that was apparently unrelated to temperature. These two sciaenids were largely responsible for the uniformity of catch seen when *Engraulis mordax* was excluded from the catch totals. The only major change in catches of *S. politus* and *G. lineatus* occurred during the October-December periods of 1979 and 1980 when CPUE was depressed. During this time of year the adults of both species presumably migrated out of our sampling area into deeper water.

Temporal distributions differed for *Scomber japonicus*, *Sarda chiliensis*, and *Sphyraena argentea*, the major higher carnivores of the assemblage. The observed temporal differences probably reflect differences in general longshore migratory patterns and residence of juveniles within the study area (e.g., presence of juvenile *S. argentea* near San Onofre kelp bed during fall-winter, authors' pers. obs.). A pos-

[5]DeMartini, E. E., and L. G. Allen. Temporal and spatial patterns of distribution and abundance of benthic, soft-bottom fishes at shallow depths off San Onofre-Oceanside, California. Manuscr. in prep. Marine Science Institute, University of California, Santa Barbara, CA 93106.

sible explanation for the virtual absence of *Sarda chiliensis* from night collections is that they may migrate offshore of 30 m depth before or at dusk on a daily basis. Net avoidance can be effectively discounted, since this fast swimming scombrid can presumably see the net better during the day than at night.

Although location differences and temporal changes were evident for some species within this assemblage, the dominant pattern shown by the most abundant species was one of a general dispersal offshore at night from nearshore diurnal schools. Diel interactions with depth were found for total individuals, total individuals minus *Engraulis mordax*, species counts, numbers of *E. mordax*, and numbers of *Seriphus politus*. Various diel and/or depth effects were also found for other taxa, including *Peprilus simillimus*, *Genyonemus lineatus*, atherinid spp., and *Scomber japonicus*. These results plus the significant correlations between species abundances and time of collection and depth underscore the general importance of diel and depth factors to the abundance and distributions of fishes in this assemblage.

Greater net avoidance under conditions of increasing water clarities, such as occur at greater distances offshore, potentially confounds our evaluation of depth (onshore/offshore) patterns. Correlations between the CPUE of major taxa and water clarity indicate persistent, negative relationships (Table 5). Variations in water clarity, however, were never observed to explain >16% of the variance in catch; and among the major taxa analyzed in detail for CPUE-water clarity relations, mean CPUE differed by more than a factor of 10 to over four orders of magnitude between the 5-11 m and 18-27 m depth blocks during the day. For this reason, we strongly feel that the potentially greater net avoidance in clearer waters farther offshore is insufficient to explain the observed daytime onshore/offshore stratification of these fishes.

Net avoidance also is a possible complicating factor to our interpretation of day-night differences in catch (i.e., higher night catches). Our test results in fact indicate an approximately twofold greater average catch efficiency for *Seriphus politus* at night versus during the day. However, CPUE of *S. politus* differed by a factor of four and by over three orders of magnitude between diel periods at the 12-16 m and 18-27 m depths, respectively. As above for the potential confounding of daytime depth patterns, we feel that diel differences in catch efficiencies alone cannot explain the marked diel patterns that we have observed.

Dispersal of schooling (especially pelagic) fishes under low light conditions has been noted repeatedly in the literature (Shaw 1961; Loukashkin and Grant 1965; Woodhead 1966; Hobson 1968). Four possible hypotheses (or a combination thereof) can be proposed to explain the phenomenon of nocturnal dispersal.

1. Schools disperse because light levels are insufficient for fish to maintain visual contact. Vision is an important factor in the maintenance of a polarized state and parallel swimming in schooling fishes (Shaw 1978). Some fishes can maintain polarized schools in light intensities as low as 0.5-0.01 footcandle (Shaw 1961), but disperse in total darkness (Shaw 1961; Loukashkin and Grant 1959, 1965). Some species have the ability to form polarized schools by the light of the full moon alone (Shaw 1961, 1978). The acousticolateralis system may also play an important role in polarization and spacing within schools (Shaw 1978) and is not dependent on light levels. Highly sensitive visual and acoustic systems may allow nearshore pelagic fishes to school even under minimal light intensities. If the visual and acoustic systems of these fishes prove to be sufficiently sensitive, an explanation for the observed nocturnal dispersal probably lies elsewhere.

2. Schools disperse because predation pressure is less intense at night. Hobson (1978) has argued that the threat from predators is a major force behind aggregating (i.e., schooling) behavior in fishes. At low light intensities pressure from visual predators such as those found in this nearshore habitat should be less. However, for this hypothesis to be valid there must be some disadvantage to schooling at night. Theoretically (Eggers 1976) and empirically (Koslow 1981), schooling occurs at the expense of prey consumption. With the threat from predators diminished at night, dispersal of fishes within a school may allow greater food consumption by lessening visual-field overlap (Eggers 1976). Dispersal under these conditions, however, would only be advantageous if the species feeds at night (see hypothesis 4 below).

3. Schools disperse offshore at night to facilitate reproduction among members. DeMartini and Fountain (1981) presented evidence for dusk spawning in *Seriphus politus* during March-August along the same stretch of southern California coastline. Crepuscular spawning probably helps conceal adults and planktonic eggs from visual predators. Unbalanced, day-night sex ratios at shallow depths[6] and egg

[6]DeMartini, E. E., and L. G. Allen. Diel and seasonal shifts in the

hydration rates (DeMartini and Fountain 1981) indicate that most male *S. politus* migrate offshore to spawn each night while individual females on average move offshore only once every week.

Engraulis mordax spawns exclusively at night (Hunter and Macewicz 1980) during its peak (January-April) spawning period. Spawning activity may be partially responsible for nocturnal dispersal in this species during this period of year. However, since most *E. mordax* in our catches were juveniles, its offshore dispersal at night is probably unrelated to spawning.

We believe that at least part of the general nocturnal dispersal pattern may be explained by the reproductive behavior of *Seriphus politus*. However, not enough is known about the reproductive habits of the other abundant fishes of this assemblage to assess the overall importance of spawning behavior to nocturnal dispersal.

4. Schools disperse at night for individuals to feed on nocturnally active prey. Hobson (1968) stated that some authors have greatly underestimated the extent to which vision can be used at night by predatory fishes. Many species of California nearshore fishes possess scotopic visual pigments which have spectral sensitivities best suited for twilight and night vision (Hobson et al. 1981). Five species that were important in our study (*Hyperprosopon argenteum*; spotted scorpionfish, *Scorpaena guttata*; *Seriphus politus*; *Xenistius californiensis*; and *Umbrina roncador*) were included in Hobson et al.'s (1981) list of fishes that forage at night. Hobson and his colleagues were able to characterize the feeding behavior of these nocturnal species through extensive field observations. Midwater planktivores oriented in a tail-down attitude in the water column at night. This presumably allowed them to feed on organisms overhead which were silhouetted against back-lighted surface waters.

Our comparison of day versus night gut fullness has assumed that most planktonic prey are evacuated from foreguts in <12 h at 14°-24°C and that any remaining contents would be in a highly digested state and, therefore, weigh less during nonfeeding periods. These assumptions seem reasonable in light of a recent determination of gastric evacuation rates in *Engraulis mordax*. At 15°C, foregut excavation rates were <30 min for small *E. mordax* larvae and about 2 h for the egg yolks and embryos of *E. mordax* (Hunter and Kimbrell 1980). Our interpretations of day-night CI's are based on the further reasonable assumption that gut evacuation rates are not seriously confounded by different digestabilities of planktonic prey eaten during the day versus at night.

Engraulis mordax has been described as a diurnal planktivore by Loukashkin (1970). However, a great deal of indirect evidence including 1) the predicted inadequacy of diurnal ration (Leong and O'Connell 1969); 2) eye and retinal morphology (O'Connell 1972); 3) size selective biting and filtering behavior (Leong and O'Connell 1969; Koslow 1981); and 4) the ability to capture and consume large copepods and euphausids (Loukashkin 1970, cited in O'Connell 1972) suggest that *E. mordax* feeds at night as well as during the day. The results of our gut fullness analysis lend support to the hypothesis of nocturnal feeding in *E. mordax*. Day-collected fishes did not contain greater amounts of food in the foregut than night specimens, which would be expected if *E. mordax* was strictly a diurnal feeder. Thus, the observed nocturnal dispersal of this species is likely due in large part to feeding behavior. It is also possible that predation pressure interacts with feeding to influence the diel behavior of *E. mordax*.

Hobson and Chess (1976) determined that *Seriphus politus* was primarily a nocturnal feeder. Schools of *S. politus* migrated offshore at night from shallow water where they had formed resting schools during the day; and specimens collected at night in open water contained large, nocturnally active zooplankters (Hobson and Chess 1976). Our analysis of gut fullness corroborates these findings. Night-captured specimens of *S. politus* contained a greater amount of (primarily mysid) prey than those of day-captured specimens. Hence we conclude that dispersal at night facilitates feeding in *S. politus*. Differential offshore dispersal of juvenile, female, and male *Seriphus politus* at night is undoubtedly related to the aforementioned breeding as well as feeding behavior.

Genyonemus lineatus probably feeds day and night as evidenced by gut fullness during both diel periods. A trend toward more food in the foregut was evident in night-collected specimens, but the difference was not statistically significant. Gut contents of *G. lineatus* collected at dawn and dusk from Long Beach Harbor have also suggested a greater amount of food in dawn-captured specimens, but, as with our study, the difference was not statistically significant at the 0.05 level (Richard N. Bray[7]). *Genyonemus lineatus*

depth distributions of immature versus adult queenfish (*Seriphus politus*). Manuscr. in prep. Marine Science Institute, University of California, Santa Barbara, CA 93106.

[7]Richard N. Bray, California State University, Long Beach, CA 90840, pers. commun. April 1982.

can be characterized as an opportunistic feeder that forages both day and night (M. J. Allen[8]). Nighttime dispersal in this species as in *Seriphus politus* could be related to feeding activity.

Results of day-night comparisons of foregut fullness in *Peprilus simillimus* were inconclusive due to the limited time period over which samples were available (June and July 1980 only). Our data nonetheless indicate that, at least during this time period, *P. simillimus* fed both day and night.

Atherinopsis californiensis appears to be strictly diurnal in its feeding activities. The observed dispersal within the inshore section of the study area probably has some other cause(s) than feeding behavior.

In summary, feeding behavior is probably an important factor related to nocturnal dispersal in *Seriphus politus*, *Engraulis mordax*, and *Genyonemus lineatus* but not in *Atherinopsis californiensis*. Crepuscular spawning may also be important in determining diel movements in *S. politus* during March through August. The cause of school dispersal in atherinids (represented by *A. californiensis*) is unknown, but deprivation of visual schooling cues and relaxed predation pressures remain as two possibilities.

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REPRODUCTION, GROWTH, AND OTHER ASPECTS OF THE BIOLOGY OF THE GOLD SPOT HERRING, *HERKLOTSICHTHYS QUADRIMACULATUS* (CLUPEIDAE), A RECENT INTRODUCTION TO HAWAII[1]

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ABSTRACT

The gold spot herring, *Herklotsichthys quadrimaculatus*, was introduced to Hawaii by unknown means probably in the early 1970s and apparently spread and increased in abundance very rapidly. On the island of Oahu, it has been regularly present in inshore areas since 1976 and has been most abundant during late spring to early fall. Among adult fishes sampled, females slightly outnumbered males in seine collections by day in shallow water, but males predominated in nighttime collections from deeper water. Both sexes began to mature at 75-80 mm SL and females carried distinct size groups of nearly mature ova by 90 mm SL. Gonad to somatic weight ratios from both sexes indicated a spring-to-fall spawning season with a midsummer peak. Batch fecundity of females was 1,100-6,300. There was no direct evidence of multiple spawning, but secondary size groups of small ova were observed in some females which also carried a distinct batch of larger ova. Holding experiments showed that juveniles deposit daily growth increments on sagittae. Age estimates from increment counts of fish 17-121 mm long indicated that herring metamorphose at about 1 month, mature at 5-6 months, and probably live no more than 1 year. The reproductive life span of females appears long enough to ripen more than one batch of ova.

Only three species of marine clupeid fishes are known to occur in Hawaii. The round herring, *Etrumeus micropus*, and the sprat, *Spratelloides delicatulus*, are both native to the islands, while the Marquesan sardine, *Sardinella marquesensis*, was introduced in the late 1950s in hopes of increasing the supply of baitfish for the local skipjack tuna fishery. The introduction was successful in that *S. marquesensis* reproduced and spread throughout the islands soon afterwards, but the species never became abundant nor contributed significantly to local baitfish catches (Murphy 1960; Hida and Morris 1963).

In 1975, small clupeids began to appear regularly in Kaneohe Bay on the island of Oahu and by 1976 had become very abundant both in the bay and apparently at other areas of Oahu. Because these fishes closely resembled Marquesan sardines and no other similar species was expected to occur in Hawaii, we blithely assumed them to be *S. marquesensis*. Their sudden obvious presence and consistent occurrence in various collections for other purposes prompted us to undertake further sampling in order to investigate their biology in Hawaii.

After the study had been largely completed, careful examination of a few specimens by W. J. Baldwin of the Hawaii Institute of Marine Biology and subsequent rechecking of our material plus more recent collections showed that we were not dealing with the Marquesan sardine, but rather with the gold spot herring, *Herklotsichthys quadrimaculatus*. No attempts to introduce *H. quadrimaculatus* to Hawaii have been reported and, although its range is uncertain due to probable misidentification in many reports, there is no evidence that it occurs naturally anywhere within ca. 3,500 km of Hawaii. Thus our study became one of an apparently inadvertently introduced species, whose introduction was considerably more successful than the more carefully planned introduction of the Marquesan sardine.

This paper summarizes available data on the introduction and spread of *H. quadrimaculatus*, briefly considers several aspects of its general biology in Hawaii, and presents results of investigations of its reproduction and growth. In the course of the latter we demonstrate that growth increments on otoliths are valid estimates of age in days as has already been shown for several temperate and tropical species including the Hawaiian anchovy or nehu, *Stolephorus purpureus* (Struhsaker and Uchiyama 1976). Although there are few comparable data on other tropical clupeids, some comparisons and contrasts of *H. quadrimaculatus*' life history pattern with those of

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other species are possible. Unfortunately, we are only able to speculate about many aspects of the introduction and subsequent spread of this species in Hawaii.

METHODS

Herklotsichthys quadrimaculatus were taken at night with small purse seines in water 12-13 m deep in the southern end of Kaneohe Bay on the island of Oahu. All sets were "blind," i.e., the net was set more or less at random within the general area to be sampled, and no lights were used to attract fish prior to the set. Most herring were taken with a 61 m long by 12 m deep seine of ca. 0.3 mm square mesh. Up to several hundred juveniles and up to 12 adults were taken per set. Between September 1974 and December 1976, 99 sets were made with this net. This series was initially intended to sample the Hawaiian anchovy. Over most of this period, samples were taken at 2-3 wk intervals; the longest interval between sampling was slightly more than a month. Most adult herring were taken with a few exploratory purse seines of a larger (153 m long by 11 m deep), coarser mesh (ca. 25 mm stretch mesh netting); this purse seine was first tested in May 1975 and set at about monthly intervals between December 1975 and December 1976. Other sporadic samples were taken with both nets during 1977-79.

Herklotsichthys quadrimaculatus were found only in shallow water (≤3-4 m) during the day and were collected by a variety of methods from several locations on Oahu. Juveniles were readily captured by small beach seines or cast nets over reef flats in Kaneohe Bay; however, to obtain adults from all seasons of the year, particularly when they were absent from night purse seine collections, we used specimens from beach seining on exposed coasts on the northeast side of Oahu as well as on reef tops in Kaneohe Bay, from baited hook or three-pronged hook "snag" fishing in harbors at Haleiwa and in Kaneohe Bay, and from bait captured in Pearl Harbor by a skipjack tuna vessel.

In addition to our collections for biological analyses, we have also examined specimens caught by others from a wide variety of habitats and locations on Oahu in order to confirm that *H. quadrimaculatus* was present all around the island. We have very few data on the occurrence of *H. quadrimaculatus* elsewhere in the archipelago and thus cannot be certain that our observations apply to all Hawaiian Islands.

Inshore areas in southern Kaneohe Bay were surveyed visually by day, and the presence of gold spot herring schools, their approximate size composition, and approximate numbers noted. Surveys were made at nearly weekly intervals from June 1978 to September 1979; prior to this time they were made sporadically and unsystematically.

Most fish were immediately preserved and held in ca. 4% formaldehyde seawater solution. Those fish used for age determination were frozen until otoliths were removed. Standard length (SL) was measured to the nearest mm and wet weight (ww) to the nearest 0.01 g after blotting dry. Dry weight was measured to the nearest 0.01 mg after 24 h at 60°C. Stomach contents of the fish were removed before drying. Sex was determined for all adults and a sample of about 200 juveniles 50-80 mm SL. Rough estimates of stomach fullness and types of prey eaten were recorded from 390 fish. When desired, gonads were dried and weighed separately. The gonad/somatic weight ratio (G/S) was calculated from the dry weight of the gonads and dry weight of the fish excluding gonads (dw_s), rather than total dry weight of the fish including gonads (dw_t).

Portions of the ovaries of mature-sized females from each month's sample were examined, and diameters of several of the largest ova measured to the nearest 0.02 mm with an ocular micrometer. For 20 females with well-developed ova, a section of the ovary containing about 200 ova >0.20 mm was teased apart and all ova >0.20 mm were measured. Preliminary data indicated no differences in ova density or size composition within or between ovaries of the same fish. The examined sections and remaining portions of the ovaries were dried and weighed separately, and the total number of ova in the largest mode was calculated from the weights of the section and remaining ovary and the ova count from the section. For 26 other females with a clearly separated mode of large ova, all ova in that mode were counted from both ovaries.

The growth increments or rings on sagittae of fish less than ca. 50 mm SL faded within a few hours to days after dissection; consequently, counts were made as soon as possible after removal from a fresh or thawed specimen. The sagittae were mounted in glycerine and rings of each counted at least three times under 100-400× magnification. Generally otolith rings from fish of this size were easy to discriminate and the repeated counts rarely disagreed; however, if a consistent count could not be made, the data were discarded.

The denser otoliths from fish >50 mm SL were allowed to air dry and then mounted in Euparol[3]. The

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

rings became clearer with time; consequently, the otoliths were stored for 2 wk, counted, and then recounted 2 wk later to confirm the first counts. On each occasion, counts were made along the rostral, postrostral, and antirostral axes, when possible. Especially prominent rings were noted and were of great use in tracking and comparing counts of the numerous closely spaced rings of large fish.

To determine if growth increments on the otoliths were formed daily, small metamorphosing herring were captured in Kaneohe Bay and held alive in shaded tanks which received a continuous flow of seawater from the bay at near ambient temperature. A subsample of the collected herring was frozen immediately after capture, and subsamples were removed from the tanks at later dates but at the same time of day (±1 h) as the original capture. The differences in numbers of rings between fish from the different subsamples were compared with the number of days elapsed. In the first two of these experiments, the fish were fed frozen zooplankton from Kaneohe Bay 3-4 times/wk on an irregular schedule, but in the last two experiments they were fed brine shrimp once or twice daily, 6 d/wk. The fish also probably ate some plankton from the seawater supply to the tanks.

RESULTS

Appearance and General Biology

Catches of the purse seine sets indicated that the gold spot herring first appeared in Kaneohe Bay in mid-1975, but did not begin spawning in the area until 1976. No herring were taken in a total of 25 sets with the small purse seine on 12 dates between September 1974 and July 1975. The first catch was an adult taken on 23 July 1975, and 11 others (66-117 mm SL) plus a 28 mm juvenile were taken in 27 sets on 11 dates between July and December 1975. In the first six months of 1976, 28 sets on 12 dates yielded 65 fully transformed herring 45-120 mm SL—most of them adults. Two of these sets (in March and April) also collected a total of 14 herring just beginning transformation from the larval stage. Catches increased markedly in the second half of the year. A single set taken in late June 1976 took 131 transforming or small juveniles (19-37 mm SL), and almost all subsequent sets with the small purse seine took herring of a wide size range. Two experimental sets with the large seine in May 1975 caught no herring. Adults (up to 120 per set) were taken in subsequent sets in April, May, and October 1976 and June 1977.

There was general agreement between collections made by others in the bay and our visual observations that gold spot herring were not present in the bay prior to mid-1975 and that recruitment of juveniles was not substantial until 1976. Adult or near-adult herring first appeared over reef flats during the day shortly after the first purse seine catches. Although our records do not unequivocally indicate whether or not juveniles were present in 1975, large schools (thousands of individuals) of transforming herring were definitely not observed until 1976. Subsequent to 1976, transforming or small juvenile herring were observed or caught in all months of the year, but were more abundant from June to November or December. In 1976-79, adults were present in catches or observations from March to December, and except for 1979 were present in abundance primarily from May to October. Their presence was, however, sporadic even during the latter months, and in 1979 few were seen or caught at any time.

Our observations in Kaneohe Bay appear to be representative of inshore areas all around the island of Oahu. Casual reports by other scientific personnel as well as by commercial and recreational fishermen indicated that "sardines" appeared and subsequently increased markedly in abundance elsewhere on Oahu at about the same times as in Kaneohe Bay and that subsequently they were most abundant from spring to fall. Unfortunately, we did not obtain any specimens of "sardines" from other areas of Oahu until late 1976, but it is extremely unlikely that the casual observations refer to the Marquesan sardine, the only species with which the gold spot herring might be confused. We have examined specimens taken in 1976-82 from a wide variety of locations on Oahu (from day collections in the surf zone to specimens taken under night lights several km offshore) and found all to be *H. quadrimaculatus*. We find no evidence that, prior to 1975, "sardines" of any sort were ever sufficiently abundant to attract attention, and the most recent specimens of *S. marquesensis* from Oahu were taken in 1968.

During the day, the gold spot herring of all sizes in Kaneohe Bay were mostly found over sand-rubble reef flats 1-2 m deep in fairly clear water or in somewhat deeper water around piers, floating docks, etc. They were absent from these areas at night. Although our nighttime purse seine sampling was inadequate to properly consider dispersion, the catches indicated that juveniles moved into deeper water at night, but tended to remain within a few hundred meters of the reef or shore. Adults were taken routinely up to 1 km away from the nearest shallow water. We have also examined adults taken under

night lights as far as 10 km offshore in water hundreds of meters deep.

Before the appearance of the gold spot herring, the dominant pelagic planktivorous fishes in Kaneohe Bay were the Hawaiian anchovy or nehu (which is the main source of bait for the local skipjack tuna fishery) and the iao, *Pranesus insularum* (Atherinidae). Although the nehu and gold spot herring cooccurred in almost all purse seine catches and adult herring occasionally eat larval or juvenile nehu (see below), there was no evidence that the herring's appearance substantially affected the nehu population. The nighttime areas of highest abundance for the two species appear to be slightly different within the bay, and nehu by day prefer more turbid, brackish areas than do the herring. The iao population, however, appears to have been affected markedly by the herring. Prior to the appearance of herring, iao were regularly present in large numbers over shallow reef flats during the day, but since have been nearly completely replaced by herring in the same situations and are much less frequently seen.

Qualitative examination of stomach contents of gold spot herring showed that they eat a wide variety of zooplankton and indicated that they feed primarily but not exclusively at night. Fish <30 mm SL (116 examined) had eaten small (<1.0mm) copepods almost exclusively. Those 30-80 mm SL (31 examined) also ate copepods but included larger zooplankton such as decapod zoeae, the pelagic shrimp *Lucifer chacei*, mysids, and small fish larvae. Adult herring (243 examined) ate copepods less frequently and larger zooplankton more frequently than did juveniles and also took considerably larger prey such as chaetognaths, polychaetes, shrimp, and fish (*Pranesus insularum* 23-25 mm SL and *Stolephorus purpureus* 6-31 mm SL). In one late afternoon sample of adults, the stomachs were mostly packed with what appeared to be planulae. Usually, however, both fullness and composition of prey in individual fish were variable even with the same sample; some fish contained several types of prey while others were mainly full of a single type. As with Marichamy's (1970) study of *Herklotsichthys punctatus*, we found no evidence that any sizes of *H. quadrimaculatus* eat phytoplankton. Overall, fresh prey was more frequent in fish caught at night and empty stomachs more so during the day, but fish in both conditions were found in almost every sample examined.

Gold spot herring apparently spawn mostly or entirely outside Kaneohe Bay. No eggs or larvae were found in any plankton tows taken in the bay while adult sardines were present; these tows included eight oblique tows taken during the peak spawning season in the same areas where adults had been collected. The smallest fish collected or observed were 17 mm SL and in the process of transforming from larvae to juveniles.

There were other movements of gold spot herring both within the bay and between the bay and exposed areas. Adult herring on several occasions vanished from all areas of the bay for varying periods and then reappeared with no obvious relation to any environmental factor. What appeared to be the same schools of juveniles were often observed in the same place for several days in a row, but before there was any observable change in size composition, the schools vanished—often to be replaced by another school of obviously different-sized fish. Similarly, the size composition of juveniles from purse seine catches showed no coherent seasonal trend.

Between 17 and ca. 30 mm SL, body depth of the transforming herring obviously increased relatively more rapidly than the standard length. Matsuura (1975) showed that in *Sardinella brasiliensis* the ossification of ventral scales is not completed until a similar size. For 50 gold spot herring 17-29 mm SL, the relationship between SL (mm) and dw_t (g), as determined by linear least squares regression on the logarithms, was

$$dw_t = 1.691 \times 10^{-9}\ \mathrm{SL}^{5.200}\ (r^2 = 0.94).$$

The relationships calculated from data for 60 juveniles 31-79 mm SL and 157 adults 80-128 mm SL were, respectively:

$$dw_t = 8.335 \times 10^{-7}\ \mathrm{SL}^{3.377}\ (r^2 = 0.98),$$

$$dw_t = 3.462 \times 10^{-6}\ \mathrm{SL}^{3.044}\ (r^2 = 0.90).$$

These differed significantly (analysis of covariance, $P < 0.01$) and indicated progressively more nearly isometric growth with increasing size. The equations for somatic weight vs. standard length differed little from those for total dry weight. Somatic weights of adult females tended to be lower than those of similar-sized males, but the difference was not significant. Wet weights of 108 fish 42-121 mm SL were related to standard length by

$$ww = 9.168 \times 10^{-6}\ \mathrm{SL}^{3.121}\ (r^2 = 0.99).$$

The relationship (based on linear least squares regression) between ww and dw_t for 123 fish 42-121 mm SL was

$$dw_t = 0.053 + 0.278\ ww\ (r^2 = 0.98).$$

Sex ratio of juveniles 50-80 mm SL did not deviate from 1:1, but there were deviations from 1:1 among larger fish depending upon time of collection. Of 348 adults from open-water night collections, the proportion of males in the total, 86.9% (95% limits: 82-91%), and in all size groups from 85 to 110 mm SL (Fig. 1) differed significantly from that expected for a 1:1 sex ratio. Males made up only 42.6% (95% limits: 37-49%) of the 392 adults from shallow-water day collections; females predominated in all size classes but one and significantly so in two (Fig. 1). The pattern in all large samples was consistent with the trend of the total collection, except for some day samples where the sex ratio was not different from 1:1. For example, a beach seine collection on a reef top in Kaneohe Bay at 1400 h in June 1977 yielded 56 males and 86 females, while a purse seine collection taken at 2000 h on the same date and 1 km away yielded 94 males and 25 females. For both the pooled collections and the above pair of samples alone, there were significant day-night differences in size composition of either sex considered separately or of the total fish collected, but there were no differences between males and females taken at the same time of day (Kolmogorov-Smirnov test, $P <$ or > 0.05, respectively). Among all the specimens examined, several females were larger (up to 128 mm) than the largest male (118 mm).

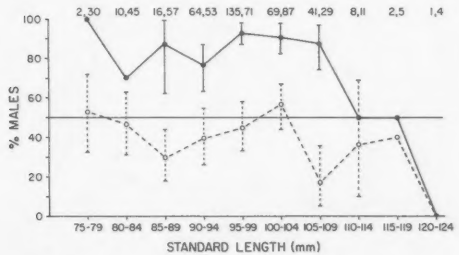

FIGURE 1.—Percentages of males among different size groups of *Herklotsichthys quadrimaculatus* for night (solid circles and lines) and day (open circles, dashed lines) collections, Kaneohe Bay, Oahu. Vertical lines indicate 95% confidence limits for observed proportions; for seven points represented by 10 or fewer fish, the limits, which included 50% (light horizontal line) were omitted for clarity. Pairs of numbers at the top represent numbers of fish of each size group examined; night collections on the left, day on the right.

Reproduction

The G/S ratios (Fig. 2) indicated that both sexes begin to mature at about 75-80 mm SL, and both the G/S and maximum ova diameters indicated that females continue to grow while ova are maturing. Although G/S values of 80-90 mm SL fish were higher than those of juveniles, values >2.5% in males and >7% in females were found only in fish >90 mm SL. With one exception, the largest ova from females <90 mm SL were <0.6 mm in diameter, while values for larger females ranged up to 0.9 mm. There was no trend in G/S or maximum ova diameter with female length for fish >90 mm SL; even during the spawning season (see below and Figure 3), the G/S ratios of some large females were almost as low as those of juveniles or presumably reproductively inactive females from winter. G/S of females was generally positively correlated with diameter of the largest ova (Fig. 2), but the relationship was highly variable. Fish carrying large numbers of small ova often had the same G/S as others carrying smaller numbers of larger ova.

Seasonal differences in G/S ratios of both males and females (Fig. 3) indicated that the principal spawning season is May-July and that at least some fish are fully mature or nearly so between March and October. Ova with yolk were not found in several of the females from August to October and in none of the 13 from November and December; yolked ova were present in all females examined from March through July. The few or no data from November to February do not preclude some spawning during the entire year, and, in fact, recently transformed juveniles about 1-mo-old (see below) were observed

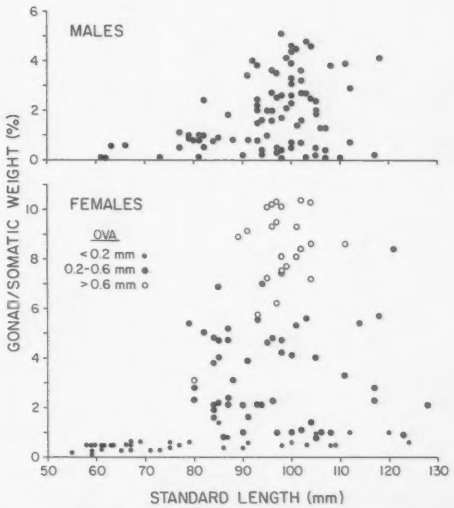

FIGURE 2.—Relationship between gonad/somatic weight and size of male and female *Herklotsichthys quadrimaculatus* collected in Kaneohe Bay, Oahu.

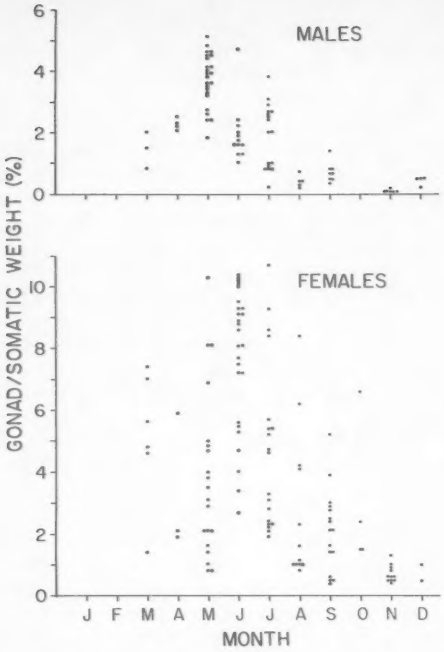

FIGURE 3.—Relationship between gonad/somatic weight and month of capture for adult (>80 mm SL) male and female *Herklotsichthys quadrimaculatus*, Kaneohe Bay, Oahu.

in Kaneohe Bay in all months. The juveniles, however, were decidedly more abundant and more frequently recorded during the summer and fall as would be predicted by a summer peak in spawning.

Our findings on ova development and size frequency in the gold spot herring are essentially the same as those of Nakamura and Wilson (1970) for the Marquesan sardine (see their figure 5). In addition to transparent ova less than ca. 0.10-0.15 mm in diameter, the ovaries of most adult female herring also contained partially yolked, semi-opaque ova ca. 0.16-0.30 mm and completely yolked, opaque ova >0.30-0.35 mm. Distinctly separated size-frequency modes of opaque ova were found from 0.30-0.40 mm to 0.60-0.90 mm. No larger, hydrated ova were found. The small, partially yolked ova were usually continuous with the smaller transparent ova; but in some fish, they formed a partially separated mode—often with opaque ova at the large end. Such modes, which were never completely separated from the smaller ova, were found in fish both with and without a separate mode of larger, opaque ova. Although a few females without a separate advanced mode had somewhat flaccid ovaries, we found no atretic ova nor any other evidence that these or any of the fish had already spawned. There was no indication of synchronous spawning or any short-term cycle; the large samples from the middle of the spawning season included females with ova in a wide range of sizes and stages of development.

In the 46 females (80-121 mm SL) with a separate advanced mode, the batch fecundity or number of ova in that mode ranged from 1,155 to 6,296 (Fig. 4). The relationships of batch fecundity to length or weight as determined by least squares linear regression were

$$F = 7{,}518.0 + 110.8\ \text{SL (mm)} \quad (r^2 = 0.84),$$
$$F = 172.0 + 218.4\ ww\ \text{(g)} \quad (r^2 = 0.79),$$
$$F = -10.2 + 795.6\ dw_t\ \text{(g)} \quad (r^2 = 0.80),$$
$$F = 21.8 + 842.1\ dw_s\ \text{(g)} \quad (r^2 = 0.77).$$

Fecundity was clearly correlated with some measure of size, but not very precisely with any of them. The appropriate equations predicted relative fecundities

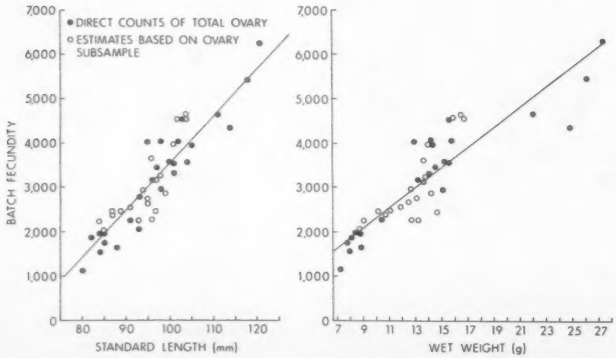

FIGURE 4.—Relationship between batch fecundity and length and wet weight of female *Herklotsichthys quadrimaculatus*, Kaneohe Bay, Oahu. Straight lines are drawn from regression equations (see text).

of 225-242 ova/g *ww* and 791-794 ova/g dw_t for the observed ranges of fish weights, while actual values ranged from 160-311 ova/g *ww* and 502-1,102 ova/g dw_t. There was no trend between relative fecundity and size.

Age and Growth

The holding experiments (Fig. 5, Table 1) provided strong evidence that growth increments on the otoliths are deposited daily. In the first experiment, there was a wide range of size and otolith ring counts in the initial and subsequent subsamples. Probably because of this, the increase in average number of rings agreed closely with the numbers of days elapsed for only two of the subsamples; otherwise, only a general trend for increase in average ring count was evident. In the second experiment, the fish were smaller and consisted primarily of two distinct groups separated by 3 mm SL and five otolith rings. These two groups were apparent in all the subsamples, and the increase for each in number of rings corresponded closely with the number of days elapsed. Since each group was about equally represented, the average difference in number of rings for the whole experiment also correlated closely with the number of days.

Both the fish and their otoliths grew faster in the third and fourth experiments, probably due to the higher feeding rate. The distance between rings was markedly greater and counts much easier to make than in the first two experiments. Fish in the initial subsample for the third experiment had a wide range of sizes and ring numbers, but a single group of fish with 26 rings dominated the initial subsample (16 of 41 fish). This group was apparent in most of the rest of the subsamples. The increase in number of rings in this group and differences in means for the subsamples corresponded closely with number of days. The results of the fourth experiment were similar. The subsample which deviated most from the predicted increase had a much narrower range of ring counts and was apparently made up mostly of the younger fish in the experiment.

Initial collections for the third and fourth experiments were made on consecutive days (31 July and 1 August 1979) from the same location and from what appeared to be the same school of transforming juveniles. In the initial subsample for the third experiment, the dominant group had 26 rings, while in that for the fourth, 13 of 39 had 27 rings (Fig. 5). Similarly, the lowest number of rings in the initial subsample for the third experiment was 23 (5 fish), and that for the fourth experiment was 24 (6 fish).

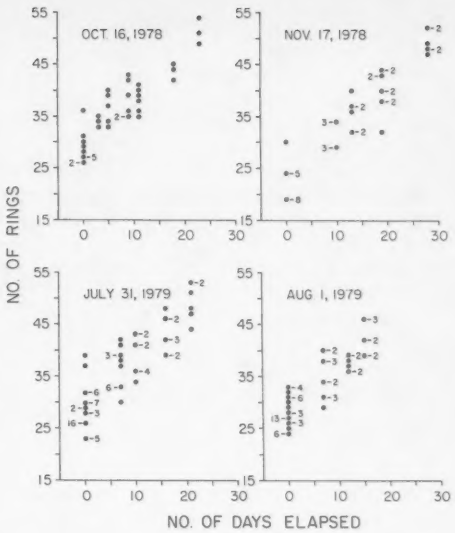

FIGURE 5.—Relationship between number of otolith rings and elapsed time for subsamples of juvenile *Herklotsichthys quadrimaculatus* from holding experiments started on four dates, 1978-79 (see text for details). Numbers of specimens are given for points representing more than one fish per subsample.

TABLE 1.—Number of days elapsed and mean increase in the number of otolith rings in subsamples of *Herklotsichthys quadrimaculatus* from holding experiments started on four different dates, 1978-79, at Kaneohe Bay, Oahu, Hawaii.

Starting date/ No. days elapsed	No. in subsample (Size range, mm SL)	Increase in mean increment count
16 October 1978		
0	12 (19.5-25.0)	0
3	3 (22.0-22.5)	5.6
5	5 (22.5-25.0)	8.2
9	6 (22.0-25.0)	9.9
11	6 (22.0-27.0)	9.8
18	3 (24.0-30.0)	15.4
23	3 (26.5-28.0)	22.9
17 November 1978		
0	14 (17.0-21.5)	0
10	6 (20.0-23.0)	9.9
13	6 (22.0-24.0)	14.1
19	9 (22.0-23.5)	18.7
28	6 (23.0-28.0)	27.8
31 July 1979		
0	41 (19.5-24.0)	0
7	14 (22.0-25.0)	7.9
10	9 (23.0-25.0)	10.6
16	8 (23.0-26.0)	14.9
21	6 (24.0-26.0)	21.3
1 August 1979		
0	39 (20.5-23.5)	0
7	11 (21.0-23.0)	7.8
12	6 (21.0-23.0)	9.5
15	7 (21.0-23.5)	14.9

Two fish in the initial subsample for the third experiment had higher counts than the maximum for the

fourth, 33 (4 fish), but the next highest value for the third was 32 (6 fish).

Although growth increments appear to be deposited daily, the age at deposition of the first ring is unknown because newly hatched gold spot herring were not available. Brothers et al. (1976) found that the northern anchovy, *Engraulis mordax*, deposits the first ring at 5 d and the grunion, *Leuristhes tenuis*, at 1 d after hatching. The otolith "age" or number of rings in the gold spot herring is probably only a few days less than the actual age, and the error for the former is substantial only for the youngest fish.

The ring counts from 106 gold spot herring 17-121 mm SL (Fig. 6) indicate that the smallest individuals were about 1-mo-old, both sexes mature at about 5-6 mo, and the largest fish was probably about 1-yr-old. Variability was high in length of fishes estimated to be older than 6 mo. There was no definite difference between males and females except that several females were both older and larger than any males.

Data suggest at least two growth cycles or stanzas. A two-cycle Gompertz-type model from Zweifel and Lasker (1976) was fitted to the data by a nonlinear least squares iteration. The equation was

$$L_t = 8.07e^{1.48\left(1-e^{-0.037A}\right)+1.37\left(1-e^{-0.013B}\right)}$$

where $A = \text{Min}(t, 59.6)$ and $B = \text{Max}(t - 59.6, 0)$ and t is the estimated age in days. The curve describes the data quite well for the fish < 80 mm, and the length at the break value for the two cycles of the curve, 59.6 d, is about 30 mm—identical to the size at which transformation appeared complete and subsequent growth more nearly isometric. The model predicts a length at time infinity of 119 mm—about the size of the largest male but well below that of the largest female. This indicates that the growth pattern for males is similar to that of juveniles, but a different curve or perhaps a third stanza may be required to describe the growth of females after maturity.

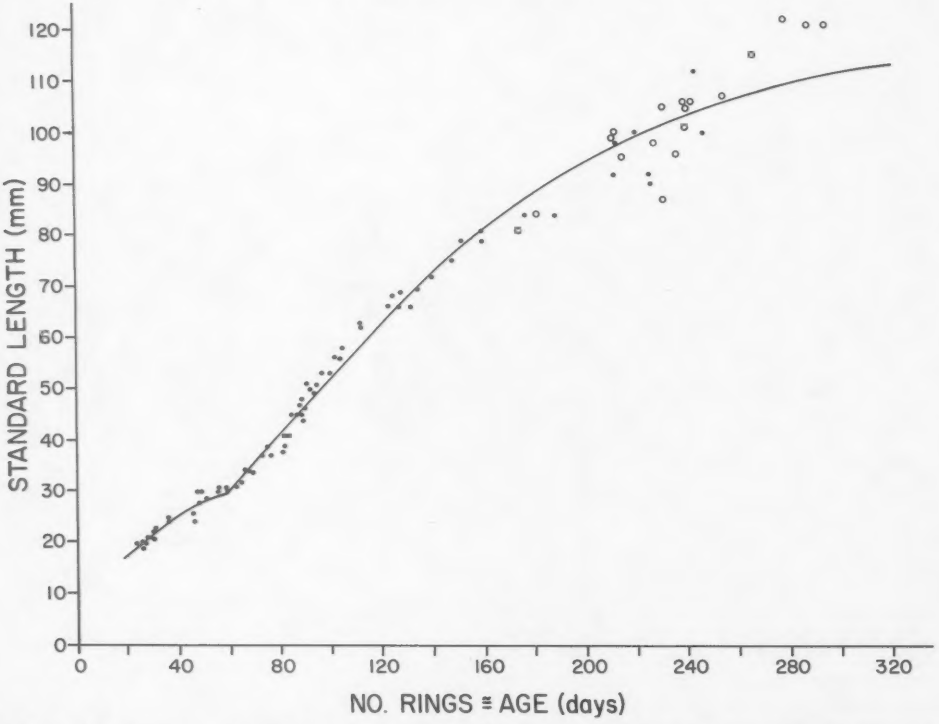

FIGURE 6.—Relationship between standard length and number of otolith rings or approximate age in days for 106 *Herklotsichthys quadrimaculatus* collected off Oahu, Hawaii. Females are indicated by open circles; solid circles represent juveniles (<80 mm SL) and males. Curve is drawn from a two-cycle growth model fitted to the data (see text).

DISCUSSION

The gold spot herring is an "annual" species which grows rapidly, but matures at an early age while small, and rarely lives more than a few months thereafter beyond maturity. Reproduction probably occurs all year, but there is a definite peak in the summer. Less extensive data on what is probably the same species[4] in the Marshall Islands (Hida and Uchiyama 1977) indicate the same life history pattern. Although seasonal changes in abundance and size composition observed in Kaneohe Bay were in part due to movements in and out of the bay, they correlate generally with the reproductive season and the 1-yr life cycle and are probably indicative of changes in the general population.

Few comparable data exist on other *Herklotsichthys* spp. or the closely related *Sardinella* spp. Maximum size in many, e.g., *H. punctatus* (Marichamy 1974) and *S. marquesensis* (Nakamura and Wilson 1970), is about the same as in *H. quadrimaculatus*. *Sardinella jussieui* (= *S. gibbosa*) and *S. brachysoma* (= *S. albella*) also appear to have a maximum age of about 1 yr (Nair 1960; Okera 1974). Other aspects of the life history of these small species may prove to be similar to those of *H. quadrimaculatus*. Within the tropics (and often cooccurring geographically with small clupeid species) some *Sardinella* spp., e.g., *S. longiceps* (Nair 1960; Ritterbush 1974) and *S. aurita* (Postel 1960), grow more than twice the length of *H. quadrimaculatus*, live for several years, and may reproduce more than one season. Such species are qualitatively more similar to the *Sardinops* spp. from higher latitudes than to the small tropical species. Following the arguments of Murphy (1968) and Leggett and Carscadden (1978), this indicates that reproductive success is more consistent in the smaller species and that even within the tropics, the basic population regulatory mechanisms of closely related species may be qualitatively different.

Data on ova development and fecundity of other species are also limited. The gold spot herring is very similar in these respects to *S. marquesensis* (Nakamura and Wilson 1970). Relative fecundity of *S. aurita* and *S. maderensis* (calculated from the respective data of Kwan-Ming 1960 and Ben-Tuvia 1960) is comparable with that of *H. quadrimaculatus*, but because of their larger size, batch fecundity in these species is much higher. *Sardinella longiceps*, however, is not only larger than *H. quadrimaculatus*, but has considerably higher relative fecundity (940-2,090 ova/g, calculated from Ritterbush 1974). These differences again indicate that reproductive success of the large species is lower or less predictable than in the small, less fecund species.

Neither our results nor those of Leary et al. (1975) on the Hawaiian anchovy offer any unequivocal evidence that these tropical clupeoids ever ripen and spawn more than one batch of eggs. The age-length data (Fig. 6) indicate that 90 mm SL gold spot herring, some of which appeared ready to spawn, are only about 1-mo older than clearly immature fish 75-80 mm SL and that females live 3-4 mo longer after reaching 90 mm SL. Thus the herring appear capable of spawning several times during their reproductive life span, but we have no evidence that they actually do so. The wide range in maximum size of ova found in herring >90 mm SL could result either from multiple spawning or variation in the size and age at which females begin to ripen ova for a single spawning. The absence of spent females indicates a single spawning and high mortality of spawners; however, no females with hydrated ova were observed either. Since spawning appears to occur away from the areas where we made our collections, it is possible that both hydration and recovery from spawning are so rapid that there is no trace of either in fishes about to leave for or just returned from spawning.

Our results, as well as those of the great majority of studies on clupeoid fishes in which appropriate data have been examined and presented, show that sex ratio of fish caught by a given gear and at a given time frequently deviates from 1:1. Assuming the actual sex ratio of adult gold spot herring is 1:1, the day-night differences in sex ratio indicate that males are more likely to move offshore at night and perhaps to remain there during the day. Such behavior is most likely related to spawning. The gold spot herring, like most other clupeoids, probably spawns at night, and Hunter and Goldberg (1980) have presented evidence that spawning schools of pelagic clupeoids are dominated by males.

Like many other clupeids, female gold spot herring appear to reach sizes larger than the largest male. Although there may be sexual differences in growth, our data indicate that female herring reach larger sizes because they live longer. If spawning incurs increased mortality due to either energy requirements or exposure to predation, the males may not live as long because they spawn more frequently than do females.

Discussion of the introduction and spread of *H. quadrimaculatus* in Hawaii is limited because we do

[4]Hida and Uchiyama identified their specimens as *H. punctatus*. W. J. Baldwin of the Hawaii Institute of Marine Biology has, however, examined numerous specimens collected from the Marshalls during Hida and Uchiyama's study and found them all to be *H. quadrimaculatus*.

not know (and probably never will) precisely when and how the species was introduced. Nevertheless, some speculations based on available data and very likely possibilities seem justified. First, it is almost certain that *H. quadrimaculatus* was not inadvertently introduced along with the *S. marquesensis* in the late 1950s. The former species is not known to occur in the Marquesas Islands, and the extensive study of Nakamura and Wilson (1970) would have likely detected it if it were actually present. The absence of any "sardines" generally and in our Kaneohe Bay samples prior to 1975, as well as the very rapid increase in abundance of *H. quadrimaculatus* between 1975 and 1976, both indicate that this species had probably not been in Hawaii very long before we collected our first specimens. Finally, the number of individuals released in Hawaii was almost certainly less than the 144,000 fish released when the Marquesan sardine was introduced (Hida and Morris 1963).

If the above speculation is close to the truth, *H. quadrimaculatus* appears to have increased from a small group of individuals to a widespread and very abundant species within a span of 2-3 yr. Even allowing for multiple spawnings per lifetime in females, the fecundity of *H. quadrimaculatus* is so low that survival from egg to adult during this period must have been extremely high. Since the population appears to have remained relatively stable since about 1976, some mechanism must have acted to lower survival rates. The most likely regulatory mechanism would be the increasing abundance of the gold spot herring themselves, i.e., intraspecific competition at some point in the life cycle. It is also possible that local predators have responded to the herring as a new resource and are presently regulating abundance.

The known differences between *Herklotsichthys quadrimaculatus* and *Sardinella marquesensis* seem unlikely to account for the former's greater success in Hawaii; to the contrary, the two species are very similar in morphology and ecology. Berry and Whitehead (1968) noted that in several respects *S. marquesensis* is more similar to the *Herklotsichthys* spp. than are other *Sardinella* spp. Fresh specimens of *H. quadrimaculatus* can be distinguished from *S. marquesensis* by the gold spots on the operculae; otherwise, close examination of the second supramaxilla, the imbedded portions of the body scales or the posterior anal rays (see Berry and Whitehead 1968) are required to separate the two species unequivocally. *Sardinella marquesensis* has higher gill raker counts than *H. quadrimaculatus*, but Nakamura and Wilson's (1970) diet data from the Marquesas indicate that, unlike most other *Sardinella* spp., *S. marquesensis* eats very little phytoplankton and, in fact, eats zooplankton equivalent to those recorded for *H. quadrimaculatus* in Hawaii. Other features of the life history of *S. marquesensis* considered by Nakamura and Wilson are almost identical to those of *H. quadrimaculatus*. Investigation of the physiology and larval ecology of the two species and, if still possible, of the ecology of *S. marquesensis* in Hawaii might better account for the greater success of *H. quadrimaculatus* in Hawaii and might also be pertinent to the broader problem of factors limiting natural distributions.

ACKNOWLEDGMENTS

We are indebted to W. J. Baldwin for correcting our initial misidentification of the topic species and to P. J. P. Whitehead for confirming the name used here. We thank T. D. Cooney for his assistance in fitting our age-length data to the growth model. This paper is based in part on V. R. Williams' Master of Science dissertation (Department of Oceanography, University of Hawaii). Partial support was derived from NSF OCE 77-09202 and from the Hawaii Institute of Marine Biology.

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AGE, GROWTH, AND SEXUAL MATURITY OF GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES* (WALBAUM), IN THE CANADIAN NORTHWEST ATLANTIC

W. R. BOWERING[1]

ABSTRACT

Age composition of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern area ranged up to 14 years for males and up to 18 years for females; most fish, however, were less than 10 years old, with a predominance of older fish in the more northerly areas. In the Gulf of St. Lawrence, males beyond age 9 and females beyond age 12 were completely absent from the catch. It is not fully clear if this is the result of emigration of older fish from the area or mortality due to early maturity. The empirical growth curves for all areas show females growing faster than the males, particularly in the older ages, while the mean size at age indicates little diffference up to ages 8-12. Statistical treatment of back-calculated growth curves up to age 5 indicated no difference between males and females. No statistical difference was found in the growth rate of fish of the Labrador and eastern Newfoundland areas. Fish from the Gulf of St. Lawrence exhibited the fastest growth rate and fish from Baffin Bank the slowest throughout the range.

Onset of maturity of female Greenland halibut from the Gulf of St. Lawrence occurred at a much smaller size and over a more narrow range of sizes than in other more northerly areas. In the Labrador-eastern Newfoundland area the onset of maturity occurred at smaller sizes, moving progressively northward. Since the growth rates of fish throughout this area are similar, this shift of the maturity curves is believed to be a result of mature fish migrating towards the spawning ground. The Baffin Bank maturity curve, on the other hand, is similar to that of Nain Bank in the mid-Labrador area. However, since Baffin Bank is so near the presumed spawning ground and heavily influenced by the cold polar current, most maturing fish are likely to be in deep warmer water outside the fishable range; consequently, the curve may be biased to the right. These inferences are supported by other investigations, particularly migration studies.

Greenland halibut, *Reinhardtius hippoglossoides*, are found in both the North Atlantic and North Pacific Oceans but absent from intervening Arctic waters (Hubbs and Wilimovsky 1964; Atkinson et al. 1981). Based on meristic and morphometric characters, Hubbs and Wilimovsky (1964) concluded that there is one species found in both oceans, not two as previously suggested (Andriyashev 1954). In the northwest Atlantic, Greenland halibut are widely distributed along the west Greenland coast and in the Davis Strait and are reported as far north as Smith Sound (lat. 78°N) by Smidt (1969) and Templeman (1973). In the Canadian far north they are found in abundance in the Baffin Island area (Templeman 1973; Bowering 1978b, 1979a) and in the Hudson Strait to Ungava Bay (Dunbar and Hildebrand 1952). They are most prevalent in deeper waters from northern Labrador to the deeper waters of the northern Grand Bank (Templeman 1973; Bowering 1977, 1978c, 1979b, 1980b; Bowering and Brodie 1981) with small numbers recorded in the vicinity of the Flemish Cap (Bowering and Baird 1980). Greenland halibut are found incidentally on St. Pierre Bank with a small localized concentration located in Fortune Bay (Bowering 1978a). Recent investigations (Bowering 1979c, 1980a, 1981) have shown that Greenland halibut have now become commercially abundant in this area with very little occurrence on the Scotian Shelf. The most southerly occurrence is Georges Bank where 20 specimens were reported caught (Schroeder 1955).

According to Smidt (1969), the main spawning for Greenland halibut in the northwest Atlantic occurs during winter in the Davis Strait area (lat. 67°N) at depths of 600-1,000 m. From here the young are believed to be carried by currents to west Greenland and eastern Canada where they colonize the banks and slopes of the continental shelf. Spawning also occurs in the Gulf of St. Lawrence in the Laurentian Channel, southwest of St. Georges Bay, during wintertime (Templeman 1973).

The commercial fishery for Greenland halibut in the Canadian northwest Atlantic is one of the most important groundfish fisheries in the region with landings averaging over 60,000 t annually during the last few years. It is of prime importance to such countries

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as Canada, U.S.S.R., Poland, German Democratic Republic, and Federal Republic of Germany, who have prosecuted this fishery for over 25 yr from Davis Strait to the northern Grand Bank and, more recently, the Gulf of St. Lawrence.

The only published information on age and growth of Greenland halibut in the northwest Atlantic was by Bowering (1978a), who reported growth in terms of arithmetic linear least squares regressions for selected areas where data were available. Walsh and Bowering (1981) presented information on the validity of field observations on sexual maturity in female Greenland halibut using histological techniques; the data, however, were confined to one area of northern Labrador. To my knowledge, this is the only available information on sexual maturity of Greenland halibut in the northwest Atlantic.

This paper presents a detailed account of the age and growth of Greenland halibut in the Canadian northwest Atlantic from Baffin Bank to the northern Grand Bank and into the Gulf of St. Lawrence. An analysis of sexual maturity data on female Greenland halibut throughout the region (except the northern Grand Bank) is also discussed.

MATERIALS AND METHODS

Age and Growth

For examination, the data were organized according to seven geographical areas: 1) Baffin Bank; 2) Saglek Bank; 3) Nain Bank; 4) Hamilton Bank; 5) Northeast Newfoundland Shelf; 6) northern Grand Bank; and 7) the Gulf of St. Lawrence, since these are discrete fishing areas where data were available (Fig. 1). All data were collected during random-stratified research vessel surveys for groundfish (Pinhorn 1972) stratified by depth. The Baffin Bank data were collected by the French research vessel *Cryos* in October 1977. This vessel is a stern trawler, 46 m long, which uses a Lofoten bottom otter trawl with a 5 mm small mesh liner in the cod end. All sets were of 30-min duration during daylight hours at a towing speed of 3.5-4.0 kn. Data from sets in which the gear was badly damaged or other reasons considered to interfere with normal retention of the catch were not used. All other data were collected by the Canadian research vessel *Gadus Atlantica*. The *Gadus Atlantica* is a stern otter trawler, 85 m long, which uses an Engels high-rise bottom otter trawl with a 12 mm small mesh liner in the cod end. All sets were of 30-min duration at 3.5-kn towing speed, and fishing was carried out on a 24-h basis.

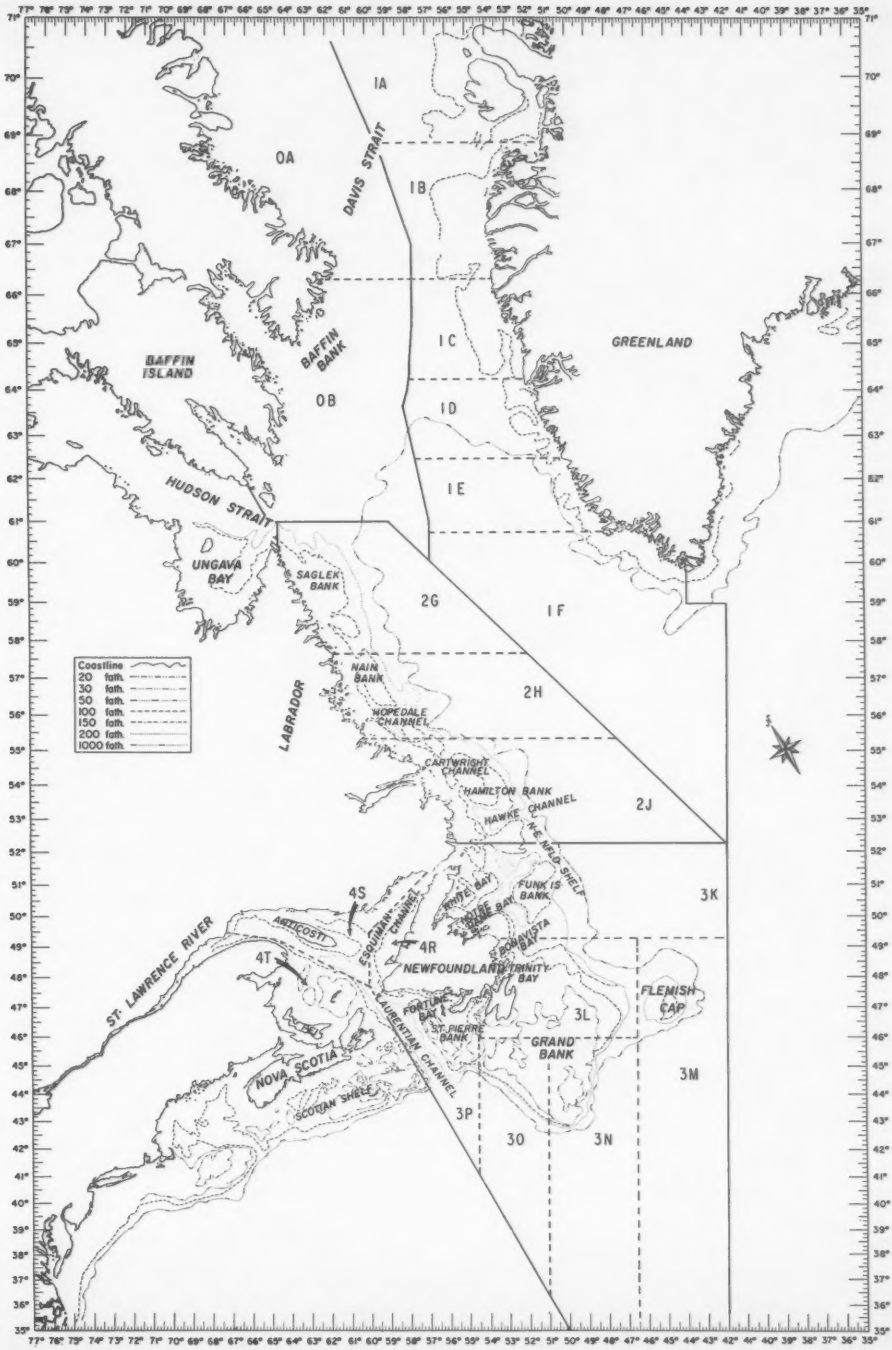
The fish ages were determined from the left sacculus otoliths which, in the case of Greenland halibut, were more suitable for age determination, since the annuli were spaced more evenly and were more distinct. Otoliths were ground on the convex surface exposing the center more clearly and were placed in a black watch glass containing ethanol in order to facilitate reading. Age frequencies were compiled for males and females separately using age-length keys for each area with the distributions calculated as numbers per thousand at age of the total catch.

For ease of statistical comparison, growth was expressed in terms of semilog curves (length $= a + b\ln$ age) similar to that used by Bowers (1960) for witch flounder and suggested in Roff (1980). Growth curves were computed separately by sex for each area. The growth curves were weighted by the number of observations at each age, since many of the older age groups were based upon as little as one observation, and the age reading of very large fish is often questionable (Lear and Pitt 1975).

Otoliths from 30 males and 30 females of the 1972 year class were selected from each area and examined to back-calculate length at age. Since the Baffin Bank data were collected in 1977 and the Gulf of St. Lawrence data were collected in 1980, only the 1972 year class was abundant enough in the samples for comparison. Subsequently, in order to standardize the number of ages for consideration, calculations could only be made up to age 5. Otoliths were measured by means of a drawing tube attached to a binocular microscope, using a technique similar to that described by Moores and Winters (1978). An annulus was considered to be the width described by an opaque (summer) zone and a translucent (winter) zone accounting for a growth increment in a particular year. The ratio of otolith length to total fish length was used to back-calculate the average length at each age, using the direct proportionality method described by Lea (1919). In order to validate the direct proportionality method as it applied to Greenland halibut, a linear least squares regression was performed on a random sample of 123 measurements of total fish length to total otolith length (3 measurements per 1 cm group from 10 to 50 cm).

A covariance analysis (Zar 1974) was performed on the back-calculated data for males versus females in order to determine if there were significant differences among the regression coefficients (slopes) or the adjusted means (y-intercepts). Where no differences between the sexes occurred the sexes were

FIGURE 1.—Map of study area with corresponding major names mentioned in text.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CARTWRIGHT CHANNEL
HAMILTON BANK
HAWKE CHANNEL
2J
N.E. NFLD SHELF
FUNK IS BANK
3K
4S
ESQUINAW CHANNEL
MISTAKEN BAY
BONAVISTA BAY
ST. LAWRENCE RIVER
ANTICOSTI
4R
NEWFOUNDLAND
TRINITY BAY
4T
FORTUNE BAY
FLEMISH CAP
3L
ST. PIERRE BANK
GRAND BANK
LAURENTIAN CHANNEL
NOVA SCOTIA
3M
SCOTIAN SHELF
3P
3O
3N
Coastline
20 fath.
30 fath.
50 fath.
100 fath.
150 fath.
200 fath.
1000 fath.

combined for each of the areas for further analysis. A covariance analysis was performed on these combined data to determine if there were any significant differences in the slopes of the fitted lines. Among the different areas, for areas where significant differences did not occur, the analysis was continued by using paired comparisons by *t*-tests to determine if differences occurred between the adjusted means (y-intercepts).

Sexual Maturity

Due to the difficulty and uncertainty connected with the determination of sexual maturity in male Greenland halibut, only sexual maturity data on female Greenland halibut were analyzed. Except for the Gulf of St. Lawrence data, only data collected during the same time of year were used to generate the maturity curves. Maturity conditions were determined by visual observations made at sea. Fish were considered mature if primary ova were visible in the ovary at any stage or if fish were in spawning or postspawning stages; otherwise, fish were considered immature.

The age or length when equal numbers of fish are mature and immature is known as the 50% maturity level or more commonly M_{50}. In assessing the effects of various dosages of poisons and vitamins on animals, Bliss (1952) devised a probit analysis method for calculating the 50% lethal dosage level (LD_{50}) which is the level where 50% of the animals are dead. Fleming (1960), Pitt (1966), and Bowering (1976) applied the same probit analysis method to determine the length at 50% maturity for cod, American plaice, and witch flounder, respectively. The only difference was that in fitting the provisional line (Bliss 1952), a closer fit was obtained by using log dosages which in the latter studies were the percentages of mature fish plotted against log length on probability paper. This modified probit analysis method was applied to the female Greenland halibut sexual maturity data from each of six areas where data were available. Since sexual maturity data for the northern Grand Bank area were so sparse, these were not included.

RESULTS

Age and Growth

Age Composition

Age composition of Greenland halibut from Baffin Bank in October 1977 showed a predominance of younger age-groups, particularly 3-5 yr olds, for both males and females (Fig. 2). Although fish were present in the catches up to age 14 for males and age 18 for females, very few fish were present beyond 8 yr old. In the Saglek Bank area, the opposite was the case with a strong predominance of fish beyond 5 yr old, although fish in the range of 3-5 yr olds were well represented (Fig. 2). Proportionally, there was a declining trend in the age-9+ groups of males from Saglek Bank to the northern Grand Bank with a marginal decline in the proportion of age-12+ females from Nain Bank to the northern Grand Bank. The most evident change in age composition over this range, however, is the abrupt change from the Northeast Newfoundland Shelf to the northern Grand Bank, particularly at ages 1 and 2. Age compositions for the Gulf of St. Lawrence data indicated very few fish less than age 4 for either sex (Fig. 2) with males absent beyond age 10 and females absent beyond age 12. The predominant age groups were 5-7 yr olds for males and 6-9 yr olds for females, all year classes of the early 1970's. It should be pointed out that since the Gulf of St. Lawrence data were collected in January and all other data collected late in the year, for comparison purposes, the Gulf of St. Lawrence data should be adjusted back by 1 yr.

Growth Curves from Observed Data

Female Greenland halibut have a longer life span than male Greenland halibut (Fig. 3). The difference in maximum age between males and females ranged from 2 yr in the Gulf of St. Lawrence to as much as 8 yr in the Saglek Bank area. It would appear from the curves (without considering mean size at age) that for all areas the overall growth rate of females is greater than that of the males. While the curves do not appear to fit the mean data points very well because of the weighting procedure, the correlation coefficients (r) were all greater than $r = 0.92$ and were all highly significant ($P > 0.001$). In almost all cases, however, the mean data points for the older ages are above the fitted lines (Fig. 3). This would suggest that if the observations were more numerous in the older ages, the computed growth rates would probably be higher than appear here, since more weight would be given to these points. As a consequence, the predicted size at age is probably only meaningful up to age 7 for males and age 10 for females. Beyond these ages, the mean size at age is increasingly higher than that determined from the fitted lines. In addition, the growth of males and females is identical up to age 7 for some areas and up to age 10 in others. It is clear that the weighting procedure underestimates relationships derived from the regression analyses compared with

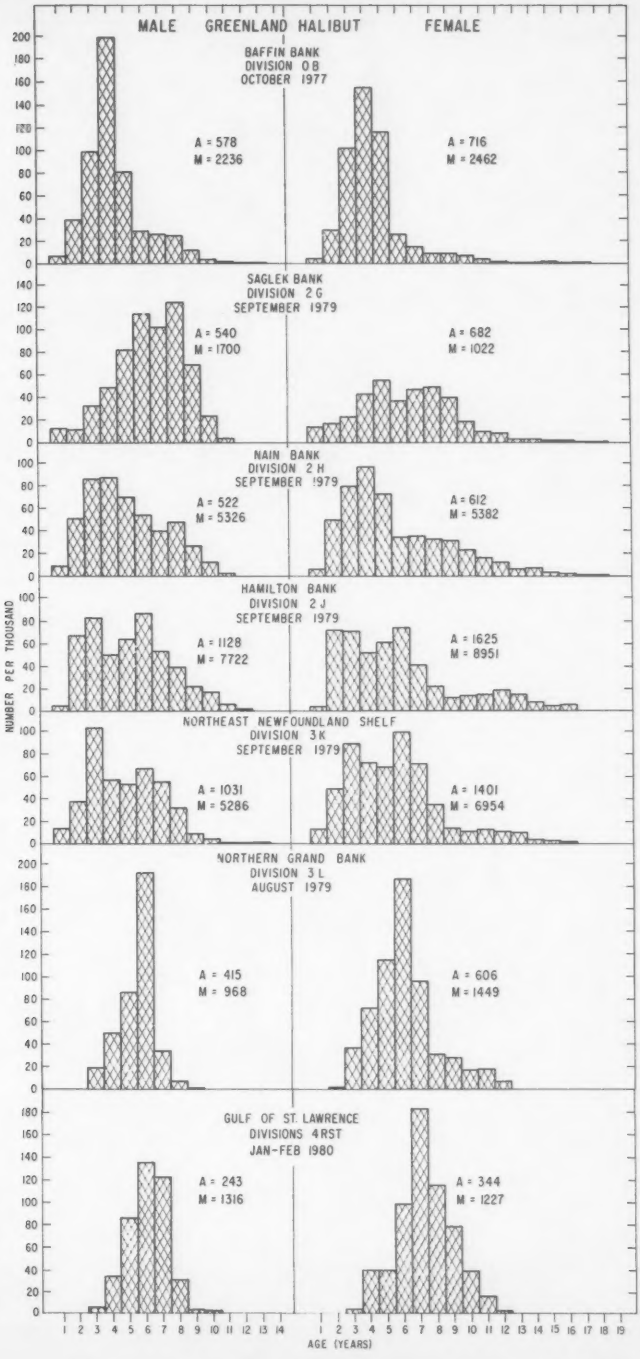

FIGURE 2.—Age composition of male and female Greenland halibut by area from Baffin Bank (NAFO Division 0B) southward to the northern Grand Bank (NAFO Division 3L) inclusive and the northern Gulf of St. Lawrence (NAFO Division 4RST).

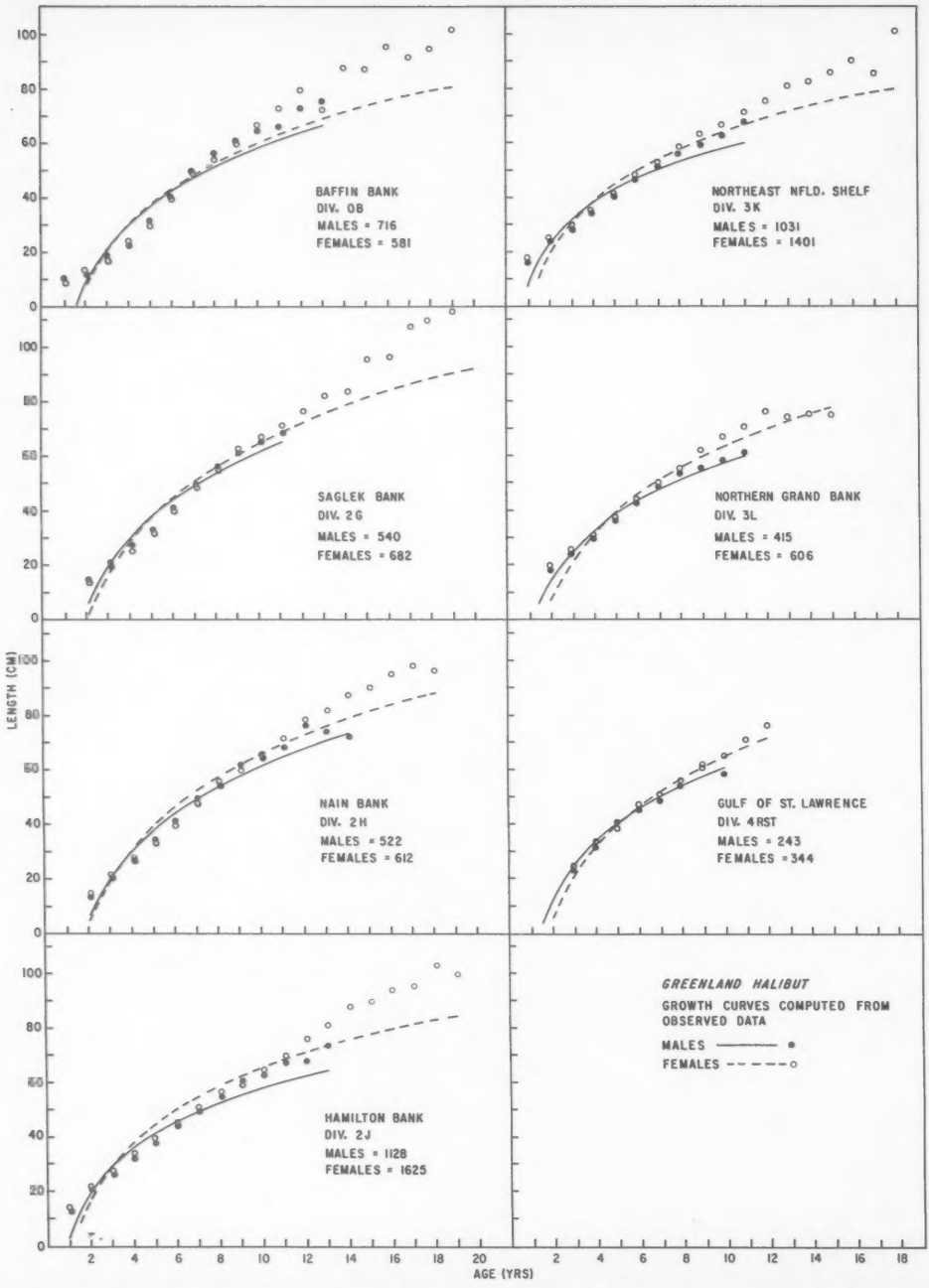

FIGURE 3.—Empirical growth curves of male and female Greenland halibut from seven areas of the Canadian northwest Atlantic.

the mean sizes at age, however, giving equal weight to each age may overestimate if given the lower numbers and questionable age readings in the very large fish.

Back-Calculated Growth Curves

The direct proportionality method (Lea 1919) for back-calculating size at age from otoliths appears valid for Greenland halibut (Fig. 4). The linear least squares regression for total fish length on total otolith length based on 123 observations yielded a correlation coefficient (r) of 0.98 and a t-value for r of 48.59 which is highly significant.

Back-calculated growth curves up to age 5 of the 1972 year class show very close agreement (Fig. 5) between males and females, particularly for the more southerly areas where the curves essentially coincide (Fig. 5). A covariance analysis of males versus females, however, indicated no significant difference in the males and females for both the regression coefficients (slopes) or adjusted means (y-intercepts) throughout the range under consideration ($P = 0.44$). The sexes, therefore, were combined. A covariance analysis on the slopes of the fitted lines for the sexes combined was performed and indicated that, with the exception of the Baffin Bank data, the regression coefficients (slopes) were not significantly different ($P > 0.05$). This would indicate that the growth rates in these areas were similar. Paired comparisons using t-tests to test for differences between the adjusted means indicated that both the Gulf of St. Lawrence data and the Nain Bank data were significantly different from those of all other areas. The Saglek Bank data differed from those of the Northeast Newfoundland Shelf but did not differ from either the Hamilton Bank data or the northern Grand Bank data. There were no significant differences amongst the adjusted means of the Hamilton Bank, Northeast Newfoundland Shelf, and the northern Grand Bank data. The combined back-calculated growth curves (Fig. 6) show the Baffin Bank growth rate to be the slowest with a considerably smaller size at age. The largest size at age is found in the Gulf of St. Lawrence with all other areas in the midrange.

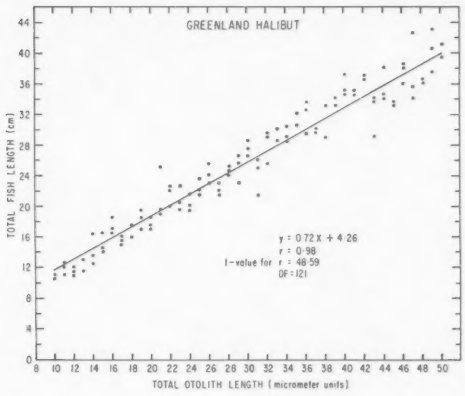

FIGURE 4.—Linear least squares regression of fish length against total otolith length of Greenland halibut.

Sexual Maturity

The sexual maturity curves (Fig. 7) indicate a clear shift to the right in the curves going from northern Labrador to southern Labrador with the Northeast Newfoundland Shelf and southern Labrador curves approximately the same. The curve for the Baffin Bank area falls near the middle (Fig. 7), close to that of the Nain Bank area. The Gulf of St. Lawrence curve, however, is well to the left and appears nearly isolated from all others.

The results of the probit transformation analysis of sexual maturity data, by area are shown in Table 1. All chi-square tests indicate acceptance of the fitted lines to the observed data at the 5% significance level. The length at the 50% maturity level, or M_{50},

TABLE 1.— Results of probit analyses of sexual maturity data for the Greenland halibut, by area, with results of χ^2 tests for acceptability of the fitted lines to the observed data.

Statistical parameter	Baffin Bank	Saglek Bank	Nain Bank	Hamilton Bank	Northeast Newfoundland Shelf	Gulf of St. Lawrence
Slope	0.1574	0.0733	0.0864	0.1118	0.1016	0.1574
y-intercept	−6.297	0.250	−1.312	−4.043	−3.086	−4.101
Length at M_{50}	71.76	64.80	73.05	80.86	79.58	57.83
χ^2 (Res. SS)	3.830	19.565	11.460	11.806	5.141	9.906
$\bar{x}$	70.57	60.70	69.82	78.85	72.52	56.07
SE M_{50}	0.2048	0.0613	0.0681	0.1237	1.7904	0.0684
SE M	0.0267	0.0058	0.0053	0.0208	0.0127	0.0127
No. fish	583	682	612	517	736	513
Age at M_{50}	10.6	9.6	10.8	12.0	12.0	7.8

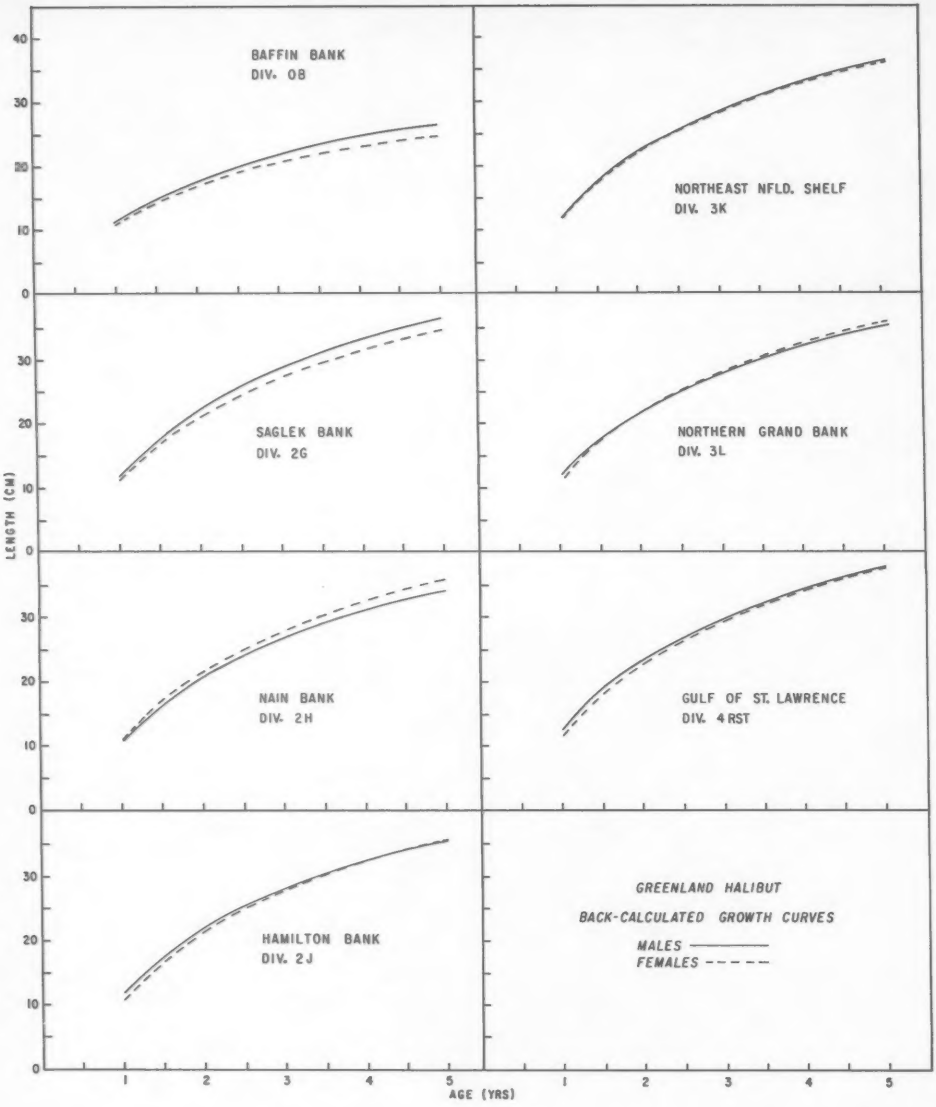

FIGURE 5.—Back-calculated growth curves (ages 1-5) of male and female Greenland halibut from seven areas of the Canadian northwest Atlantic.

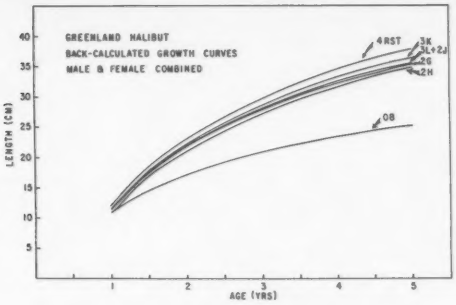

FIGURE 6.—Comparisons of back-calculated growth curves (ages 1-5) of Greenland halibut, sexes combined from seven areas of the Canadian northwest Atlantic.

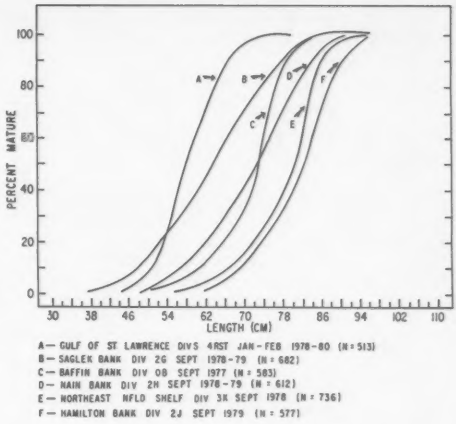
PERCENT MATURE
LENGTH (CM)
A
B
C
D
E
F
A— GULF OF ST LAWRENCE DIVS 4RST JAN-FEB 1978-80 (N = 513)
B— SAGLEK BANK DIV 2G SEPT 1978-79 (N = 682)
C— BAFFIN BANK DIV 0B SEPT 1977 (N = 583)
D— NAIN BANK DIV 2H SEPT 1978-79 (N = 612)
E— NORTHEAST NFLD SHELF DIV 3K SEPT 1978 (N = 736)
F— HAMILTON BANK DIV 2J SEPT 1979 (N = 577)

FIGURE 7.—A comparison of sexual maturity ogives of female Greenland halibut from six areas of the Canadian northwest Atlantic.

decreased from 71.8 cm in the Baffin Bank area to 64.8 in the Saglek Bank area; however, the length at M_{50} increased to 73.1 cm in the Nain Bank area and then to 80.9 cm in the Hamilton Bank area. The length at M_{50} for Northeast Newfoundland Shelf area was 79.6 cm, very similar to the Hamilton Bank value. The lowest length at M_{50} was 57.8 cm for the Gulf of St. Lawrence.

The ages at M_{50} calculated from the growth equations of Bowering (1978a) showed the same trends as did the lengths at M_{50}. The lowest age at M_{50} was 7.8 yr for the Gulf of St. Lawrence data to a maximum of 12 yr for both Hamilton Bank and Northeast Newfoundland Shelf. The results of the covariance analyses for testing the regression coefficients (slopes) and elevations (*y*-intercepts) of the fitted lines are shown in Table 2. The slope of the Baffin Bank data differed from that of Saglek Bank and Nain Bank but not from those of any other areas. The slope of the fitted lines for Saglek Bank, Nain Bank, Hamilton Bank, and Northeast Newfoundland Shelf did not differ significantly. Biologically, this means that the proportional increase of mature fish from one size group to the next were the same for these areas. The slope of the Gulf of St. Lawrence data differed significantly from those of all areas except Hamilton Bank and Baffin Bank. For paired comparisons which did not yield significant differences between the slopes of the fitted lines, statistical treatment of the elevations (*y*-intercepts) indicated highly significant differences between the intercepts for all pairs at the 1% significance level (Table 2). This means that although the proportional increase of mature fish from

TABLE 2.—Matrix of *t*-values for paired comparisons of sexual maturity data for Greenland halibut.

	Saglek Bank		Nain Bank		Hamilton Bank		Northeast Newfoundland Shelf		Gulf of St. Lawrence	
	0.0733 Slope	0.250 Int.	0.0864 Slope	−1.312 Int.	0.118 Slope	−4.043 Int.	0.1016 Slope	−3.086 Int.	0.1574 Slope	−4.101 Int.
Baffin Bank										
t	[1]2.404	N/A	[1]2.455	N/A	1.154	[2]−2.977	1.959	[2]−10.748	−0.0001	[2]−11.484
df	28	27	18	19	20	21	19	20		
Saglek Bank										
t			1.634	[2]8.311	1.877	[2]14.947	1.586	[2]13.824	[2]5.905	N/A
df			39	40	30	31	32	33	31	
Nain Bank										
t					1.394	[2]10.775	1.008	[2]7.958	[2]5.604	N/A
df					29	30	31	32	30	
Hamilton Bank										
t							0.426	[2]−4.619	1.918	[2]−6.643
df							22	23	21	22
NE Nfld. Shelf										
t									[2]2.923	N/A
df									23	

[1]Indicates rejection of H_0 at = 0.05.
[2]Indicates rejection of H_0 at = 0.01.

one size group to the next was the same, the range of the size groups themselves was different. In biological terms, this means that there is a significant difference in the size at M_{50} for all areas tested. Subsequently, the ages at which Greenland halibut reach the 50% maturity level are also different for these areas.

DISCUSSION

Age and Growth

Age composition of Greenland halibut varied throughout the range under consideration. It was apparent (although not greatly pronounced) from the age distribution that the older fish were proportionately more abundant in the more northerly areas and, according to Bowering (1978c), are more abundant in deeper waters. The large numbers of young fish in the Baffin Bank area suggest that this area may be a nursery area as indicated by Atkinson et al. (1981). However, the lower numbers of large Greenland halibut in the Baffin Bank survey may also be due to the ineffectiveness of the fishing gear at great depths (>500-700 m), since the vessel is comparatively small for fishing such depths. Chumakov (1975) found that the oldest individuals throughout the range studied here are located in waters >800 m deep in the northern region of Baffin Island (which he considered to be on or near the spawning grounds). Berth et al. (1979), in reporting results of a survey for Greenland halibut throughout the same area in December 1978, also found that young Greenland halibut increased in abundance with increased distance from the more northerly areas. Berth[2] also found that mature individuals are more abundant in the more northerly areas, suggesting a northward migration of maturing Greenland halibut for spawning. Subsequently, Templeman (1973) indicated that pelagic larvae are carried from there by the polar currents to the banks of west Greenland and eastern Canada.

The absence of Greenland halibut less than age 4 from the Gulf of St. Lawrence is difficult to explain. It may be that the young fish move to a different area than that surveyed in winter or, for some unknown reason, they are inaccessible to the fishing gear. It may be possible that if there is immigration into the Gulf of St. Lawrence from outside as suggested by Bowering (1980a, 1981), it may not include Greenland halibut in the very young age groups. The reporting of numerous 1-group Greenland halibut in summer of 1980 by Tremblay and Axelsen (1981) may in fact simply be the result of a very strong anomalous year class produced by a resident population of Greenland halibut within the Gulf of St. Lawrence. Furthermore, Bowering (in press) indicated that recruitment to the Gulf of St. Lawrence fishery was higher than that which could be expected from the stock of mature fish in the gulf. Therefore, most recruitment would have to come from elsewhere. Evidence from electrophoretic studies (Fairbairn 1981) also supports this hypothesis. Fairbairn (1981) concluded that Greenland halibut in the Gulf of St. Lawrence support a separate breeding stock with some gene flow (migration) between the Gulf of St. Lawrence area and the Northeast Newfoundland Shelf area, probably through the Strait of Belle Isle. It would appear then that the Gulf of St. Lawrence Greenland halibut population is composed of a small stock that spawns there and immigrants from the Labrador area that may emigrate to the north for spawning.

Growth Patterns

Differences in growth rate between males and females are generally the result of genetics which determine the physiology and behavior of the fish rather than the result of the environment (Alm 1959), since the males and females presumably are subjected to the same set of environmental conditions. These differences are generally the result of a diversion of energy towards the formation of the sex products with less energy available for growth, according to Alm (1959). Bowering (1978a) expressed growth of Greenland halibut in terms of linear least squares regression, since most fish in the study were immature and showed little or no diversion in growth patterns of males and females. Because of this, it was considered that the study only dealt with that section of the growth curve below the inflection point, and consequently estimates of L_∞ for the traditional von Bertalanffy growth equation were not realistic and could not be used. Results of back-calculated growth curves up to age 5 in this study resulted in no statistical difference between males and females, which in essence would support Alm (1959) and Bowering (1978a). Furthermore, the mean size-at-age points from the empirical data suggest that the difference in growth patterns between males and females would not be readily observed until in the range of 8-12 yr olds. These data suggest that, with the possible exception of the Gulf of St. Lawrence, the influence of sexual maturity on growth patterns in these areas was

[2]U. Berth, Senior Scientist, Institut fur Hochseefischerei and Fischverarbeitung, 251 Rostock-Marienehe, German Democratic Republic, pers. commun. October 1978.

negligible. Statistical comparisons could not be made with Bowering (1978a), since the data could not be standardized.

Covariance analyses on the back-calculated growth data indicated that the growth rate throughout the entire area, with the exception of the most northerly Baffin Bank area, was the same. The growth rate from the Baffin Bank data was considerably lower than all other areas. Analysis of the adjusted means (intercepts) indicated that the average size at age for the Gulf of St. Lawrence data was significantly higher than all other areas. Since the overall growth rate was the same as other areas, this would imply that the growth rate of the Gulf of St. Lawrence fish was substantially higher in the first year of life compared with other areas. While the size at age from Nain Bank was significantly different from all areas, it did not appear to vary greatly from the adjacent Labrador and eastern Newfoundland areas. Since differences between growth patterns from Saglek Bank and other areas are not totally variable, they may be a result of the location and behavior of the fish in the first year of life throughout the range.

Because there appears to be a general increase in average size at age from north to south, temperature would appear to be a contributing factor. Templeman (1964) indicated that the volume of warmer waters increased from north to south because of the direction of the Labrador Current so that temperature may have an influence on growth pattern. Any influence would have to be particularly related to the first year of life, since older Greenland halibut are known to migrate over long distances (Nizovtsev 1970; Chumakov 1970; Sigurdsson 1977), as well as vertically in the water column (Lear 1970; de Groot 1970), making them subject to a wide variety of temperatures. This may explain the high growth rate in the first year for the Gulf of St. Lawrence fish where temperatures are considerably higher than the eastern areas. It should be pointed out, however, that these growth patterns are based mostly upon immature individuals, and the difference in growth patterns of the immature individuals alone may simply be a result of conditions where they grew prior to maturity. Upon approaching maturity they could all still return to a common breeding area and be part of the same original stock.

Sexual Maturity

The commercial fisheries for Greenland halibut on the banks and slopes in the northwest Atlantic are mainly composed of immature fish (Chumakov 1975; Zilanov et al. 1976; Templeman 1973; Berth et al. 1979; Bowering 1977-81). The scarcity of mature fish in the commercial, as well as research, catches led to consideration of the possible misinterpretation of maturity condition of the ovaries, particularly by visual observation. Walsh and Bowering (1981) studied the problem histologically and concluded that while the accuracy of visual observations of sexual maturity of female Greenland halibut may be enhanced by histological analysis, for practical purposes, field observations on the onset of first maturity are adequate. Maturity of male Greenland halibut was not included in the analysis here, since it was extremely difficult to determine whether males with growing gonads were maturing for the upcoming spawning season or later. This uncertainty was probably a result of the timing of the surveys when milt was not present in the testes and previously spawned fish may have been fully recovered.

The results of probit transformation analysis indicated that the 50% maturity level (M_{50}) was reached at a much smaller size for the Gulf of St. Lawrence fish, whereas there was a trend of increasing size at M_{50} for fish from northern Labrador to the southern Labrador-Northeast Newfoundland Shelf area. Covariance analysis indicated that for the Labrador-eastern Newfoundland areas the rate of increase in the proportion of mature fish from one size group to the next was the same. The Baffin Bank and Gulf of St. Lawrence data differed from some areas but not from others. More importantly, however, were the significant differences in the intercepts of the fitted lines for all areas. In biological terms this indicates a significant difference in the sizes and ages of M_{50} for all areas.

Molander (1925), in studying European plaice and flounder in the Baltic, found that with increased growth rate, maturity occurred at a lower age but at a greater length. Bowering (1976) found similar results for witch flounder in the northwest Atlantic. Pitt (1975) indicated for American plaice that faster growing fish matured at an earlier age but all matured at approximately the same size, suggesting that sexual maturity is probably dependent on size, and indirectly on growth rate, rather than on age. From experimental research on sexual maturity of fishes, Alm (1959) concluded that "with an initially good growth rate maturity is reached at an earlier age than an initially poor growth rate. The metabolic processes are probably relatively fast with good growth rate. Consequently, differentiation processes in gonads and maturity apparently occur much earlier, the opposite being the result of poor growth rate."

The results reported here support in part the conclusions of Alm (1959). Greenland halibut from the

Gulf of St. Lawrence exhibit the highest growth rate and mature much earlier than fish from other areas. Conversely, the population of Greenland halibut from Baffin Bank exhibits the slowest growth rate, and maturity is reached at a later age than those from the Gulf of St. Lawrence. The initial growth rate of the Labrador-eastern Newfoundland areas has been shown to be very similar, occurring somewhere between those of the Baffin Bank and the Gulf of St. Lawrence. However, the size and age at maturity decrease significantly from south to north, contrary to the above theory. The reason for this may be explained if a northward spawning migration occurs. If this is the case, then it would be expected that the proportion of maturing individuals in catches at any particular size up to 100% mature would be greater, moving progressively northward. This would result in a shifting of the maturity curve to the left going north and subsequently producing lower values of M_{50}. This would further suggest that in the Labrador area the value of M_{50} for Saglek Bank may be in fact more representative of the entire Labrador-eastern Newfoundland area. The value of M_{50} for Saglek Bank falls between that of the Gulf of St. Lawrence and Baffin Bank data as does the initial growth rate. This would then be in agreement with Alm's (1959) theory of the relationship of maturity and initial growth rate.

Recent investigations by Chumakov (1982) also found that the abundance of larger mature fish increased moving northward. From tagging studies in eastern Newfoundland, Chumakov (1982) found that Greenland halibut migrated northward over long distances, from the southernmost parts of the area to the spawning grounds located in Davis Strait. He also indicated that having reached the spawning grounds, mature fish would not return to the areas where they had been dwelling before maturation. The proportions of mature fish in the more southerly areas would therefore be expected to be slowly moving southward, as shown in the data presented here. Furthermore, Bowering (1982) also studied migrations of Greenland halibut in the same area. For Greenland halibut tagged in White Bay, Newfoundland, (Fig. 1) the returns mostly came from deep waters along the continental slope of Labrador to as far north as the waters off Baffin Island near the known spawning grounds. This further suggests a northward migration of prespawning Greenland halibut.

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POWER PLANT IMPACT ASSESSMENT: A SIMPLE FISHERY PRODUCTION MODEL APPROACH

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ABSTRACT

The relative abundance of a cohort affected by power plant entrainment mortality as a fraction (R_e) of the abundance of that cohort in the absence of power plant impact can be calculated by $R_e = \exp(-E_i t_i)$ where t_i is the duration of life stage i, and E_i is the entrainment mortality rate at stage i. Rate E_i can be estimated by the ratio of nonsurviving entrained organisms during a given time interval to the mean standing crop of stage i organisms in the source water during that interval. An estimate of adult abundance allows calculation of equivalent adult losses. When insufficient information is available to determine the long-term effect on the population, the fishery "potential yield" formula provides an interim estimate. Relative equilibrium abundance of the affected population (R_e) is approximated by $R_e = 1 - (\Sigma E_i t_i + F_p + F_f)/2M$, where F_p is adult mortality rate due to power plant impingement, F_f is adult mortality rate due to fisheries, and M is adult natural mortality rate. As in the case of the "potential yield" formula, this approximation of long-term equilibrium impact should be discarded when better estimates can be developed.

In recent years considerable effort has been expended in evaluating the impact of fish removals by intake cooling water systems at power plants in the United States. Methods of impact assessment are as diverse as the power plant sites at which the studies have been conducted, but may generally be classified into those which, according to Hackney et al. (1980), 1) offer an "expert" opinion as to the presence or absence of impact, or 2) are fish population models in which the sensitivity of the source water fish populations are examined under varying impingement rates.

The first category of assessments generally attempts to compare losses of organisms owing to power plant operation with sport and commercial fishery harvests and/or estimates of standing stock (DeMartini 1979). For adults, which are subject to impingement, comparison is fairly straightforward. However, for eggs and larvae, which are subject to entrainment, meaningful comparison is less direct. Goodyear (1978) extended a method proposed by Horst (1975) for treating entrained larvae in terms of equivalent adult losses which may then be considered alongside losses because of impingement. The second category of assessments includes more complex models using Leslie matrices (Vaughan and Saila 1976; Horst 1977; Vaughan 1981), differential equations (Hackney et al. 1980), or stock-progeny-recruit models (Christensen et al. 1977).

Several problems are inherent in many of these methods. There is an absence of an impact "scale" which enables the investigator to judge objectively the significance or insignificance of fish removals relative to the source water stock and to removals by fisheries. Additionally, sophisticated methods such as Leslie matrices and Goodyear's (1978) calculation of equivalent adult losses require life history parameters (i.e., fecundity, survivorship), which are often unknown for the species in question, and require substantial expenditures of time and money to obtain. Finally, these models may be difficult to interpret. While the investigator may understand the subtleties of interpretation, agency reviewers often lack the technical background to evaluate the results of complicated models.

The approach presented in this paper will alleviate many of the above problems. The proposed methods draw on techniques and models used in fishery management in order to provide a criterion for significance of impact. Indeed, the objectives of fishery stock assessment are very similar to those of power plant impact assessment. In both cases, we wish to know the effect of removals relative to what the stock can sustain through its density-dependent or other compensatory mechanisms. The models we propose do not require detailed life history information, and are sufficiently simple that the assumptions are apparent and results can be interpreted accordingly.

The methods may be separated into two somewhat independent analyses. The first is short-term assessment, which estimates entrainment impact on a

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single cohort (e.g., year class) in the sense of Goodyear's (1978) equivalent adult mortality. The second analysis estimates the long-term equilibrium impact of combined removals, including entrainment and impingement by one or more power plants, and all other nonnatural removals, including fishery harvests.

SHORT-TERM IMPACT

In the natural state, where no spawning products are removed by entrainment, the adult abundance of a cohort, N'_c (at a reference age T), is given by

$$N'_c = Pe^{-\int_0^T \mu(x)dx} \quad (1)$$

where P is initial production of newly spawned eggs, x is age, and $\mu(x)$ is per capita natural mortality rate at age x, i.e., $-dN(x)/Ndx$.

A more convenient approximation of Equation (1) is

$$N'_c = Pe^{-\Sigma M_i t_i} \text{ and } T = \Sigma t_i \quad (2)$$

where t_i is the length of age interval i, and M_i is a per capita natural mortality rate, assumed to be constant over interval i.

In the presence of mortality due to entrainment, the adult abundance of the impacted cohort, N_c (again at reference age T) is given by

$$N_c = Pe^{-\Sigma(E_i+M_i)t_i} \quad (3)$$

where E_i is the per capita rate of entrainment mortality during age interval i.

The abundance of an impacted cohort relative to an unimpacted cohort is denoted R_c, and is given by

$$R_c = N_c/N'_c \quad (4)$$

and after substituting Equations (2) and (3), this simplifies to

$$R_c = e^{-\Sigma E_i t_i} \quad (5)$$

which is related to the conditional mortality rate (m) described by Ricker (1975: equation 1.9; here $m = 1 - R_c$). Note that T need not be specified, since we now need sum over only those age intervals in which E_i is nonzero. This is convenient since fish often cease being entrained at about the same time they cease being available to plankton sampling gear. More important is the fact that Equation (5) requires no knowledge of life history parameters. The main assumption here is that there is no compensatory change in the per capita rate of natural mortality during early life stages which offsets the added effect of entrainment mortality.

Equation (5) is similar in concept and derivation to recently published methods of calculating impact rate (e.g., Boreman et al. 1981; Jensen and Hamilton 1982). Those methods explicitly include water volumes and are especially appropriate to cases of highly fluctuating water flows. For the purposes of the assessment methods discussed in this paper, either method of calculating impact rate is applicable.

The entrainment mortality rates, E_i, are fairly easy to estimate. Larval mortality may be assumed to conform to a "Type 2 fishery" in the sense of Ricker (1975), wherein natural mortality occurs along with entrainment, and each occurs at a constant per capita rate during each age interval i. If power plant activity is fairly constant over the spawning season, each E_i is constant, and it is unnecessary to distinguish between Ricker's two types of recruitment. According to Ricker's (1975) equation 1.17, the quantity of larvae at stage i removed during a unit time by entrainment (L_i) is related to the mean abundance of larvae at stage i in the source water ($\bar{L}_i^*$) by the equation

$$L_i = E_i \bar{L}_i^* \quad (6)$$

Therefore, E_i may be estimated by the equation

$$E_i = L_i/\bar{L}_i^* \quad (7)$$

where L_i is a direct in-plant sample estimate of the quantity of stage i larvae entrained per day (or other convenient short time interval), and $\bar{L}_i^*$ is an estimate of the mean standing crop of stage i larvae over that same time interval in the source water, which may be estimated by quantitative plankton net tows. Note that entrainment rate E_i has units of inverse time according to the time interval used. Care must be taken to assure that time units are consistent throughout the analysis. Also note that i now refers to a stage, as it is generally most convenient to sort samples or planktonic larvae by size or stage categories. The length of time spent in each size category must also be determined. The most direct method may be to examine larval otoliths for daily growth rings (see Brothers et al. 1976) in order to ascertain the number of days (or other time unit employed) spent in stage i. Lacking this direct information on t_i, it may be necessary to assume that the larvae grow at the same

rate as does some better known similar species in a similar environment.

Equivalent adult loss from a cohort (A_c) may be defined as

$$A_c = N'_c - N_c. \tag{8}$$

However, a standing stock of adults often consists of several cohorts. Under the common fishery assumption that the age composition of the standing stock is at equilibrium, overall equivalent adult losses (A_e) from the stock are given by

$$A_e = N' - N \tag{9}$$

where N' denotes unimpacted stock abundance, and N denotes impacted stock abundance, given the same initial production of eggs. Although this equilibrium assumption is often violated, it is nonetheless the basis of management of many fish stocks. Since the quantity R_c describes the ratio for a cohort N_c/N'_c, under equilibrium it also describes the population ratio N/N', here denoted R. The latter may be substituted into Equation (9) to give

$$A_e = N' (1 - R) \tag{10}$$

or

$$A_e = N \left(\frac{1}{R} - 1\right). \tag{11}$$

Thus equivalent adult losses can be calculated if adult abundance has been estimated, and this does not require the extensive knowledge of life history parameters demanded by Goodyear's (1978) approach.

Equations (10) and (11) raise a dilemma with respect to short- and long-term impact. Estimation of short-term impact has been based on the assumption of a fixed initial production of eggs. However, when real data are used, preimpact abundance (N') will usually arise from a larger egg production than does postimpact abundance (N), for the very reason than N' is larger than N, and egg production is itself dependent upon adult abundance. For this reason, Equation (10) is misleading, and will tend to overestimate the amount of adult equivalent losses actually occurring from an impacted stock at equilibrium. However, in most cases, preimpact abundance is unknown, and sampling programs produce estimates of N, which require application of Equation (11). Moreover, Goodyear's (1978) equivalent adult losses are calculated for an impacted stock making Equation (11) appropriate. As will be seen below, our method of estimating long-term equilibrium impact does not require explicit calculation of equivalent adult losses, and avoids the above complications.

LONG-TERM IMPACT

Whereas short-term impact may be described in simple terms of adult equivalent losses, long-term impact is more difficult to quantify. Short-term loss of adults implies loss of reproductive potential (egg production), and this loss is compounded over several generations. If compensatory mechanisms were not present, the impacted population would decline exponentially to extinction, given that it was in equilibrium prior to the impact. Fortunately, there are many types of compensatory mechanisms that allow the population to augment its reproductive rate so that it reaches a new equilibrium in the presence of an increased mortality rate (see Goodyear 1980). For example, lowered adult abundance may lead to increased per capita fecundity, decreased age of first reproduction, and/or increased survivorship at various life stages. Unfortunately, the actual mechanisms are poorly known and can be seldom quantified even for well-studied species. Detailed knowledge cannot be expected in routine impact analyses. Rather, we need simple approximations that will require a minimum of data.

Fishery management has long been concerned with the effect of removal (harvests) rates on fish abundance. Most of the work has been concerned with long-term equilibrium, and many fishery models are directly applicable to impact analysis. In particular, the "production model" (see Ricker 1975, Chapter 13), by means of simplifying assumptions, requires minimal knowledge of life history parameters. One of the simplest production models is the Graham-Schaefer model, which is constructed on the assumption of logistic population growth. The model assumes that equilibrium stock abundance declines linearly with an increasing rate of harvest (fraction of stock removed per unit time). The maximum net productivity in terms of total harvest by a fishery is therefore assumed to be achieved at a stock size which is exactly one-half the virgin level of abundance or carrying capacity, K (Fig. 1).

Normally, the production model is useful when a long time series of catches and fishing efforts (rates of removal) is available. In such cases, the production curve can be estimated from the data by statistical regression. On the other hand, there are many fisheries for which there is no history of exploitation, or for which the required data were never collected. Here, we may draw on the "potential yield" formula, first proposed by Alverson and Pereyra (1969), promulgated by Gulland (1970, 1971), and critically reviewed by Francis (1974). This approximation assumes that net productivity is maximal when abun-

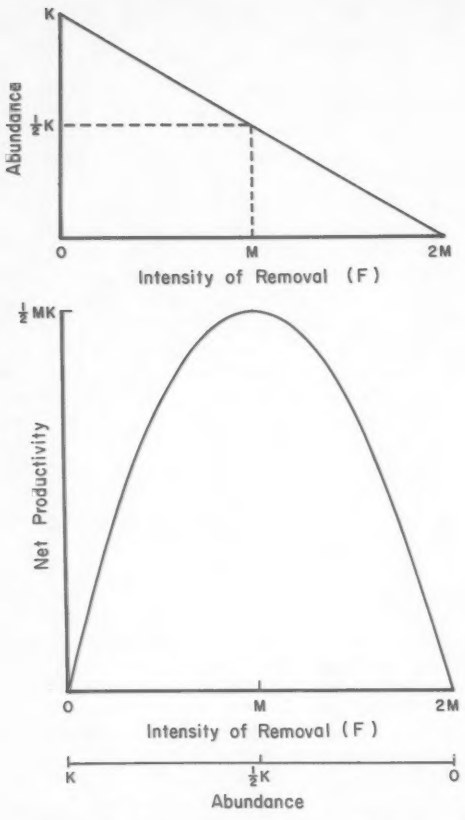

FIGURE 1.—The Graham-Schaefer production model scaled according to the "potential yield" formula (K is virgin abundance or carrying capacity, M is rate of natural mortality).

dance is at one-half the virgin level, and at this point the rate of fishery removals (F) is equal to the rate of natural mortality of adults (M). While many criticisms can be leveled at the potential yield formula, in actual practice it is often the only available basis of fishery management (e.g., North Pacific Fishery Management Council 1979a, b; Pacific Fishery Management Council 1982).

The production model corresponding to the potential yield formula is shown in Figure 1. The assumed relationship between equilibrium abundance (N_e) and rate of removal (F) is linear, giving the usual parabolic yield curve. Equilibrium abundance is at carrying capacity (K, denoted N'_e in this paper), when there are no removals. From inspection of Figure 1, the model predicts that equilibrium abundance falls to zero when the rate of removals is twice the rate of adult natural mortality (M). Thus, based on linearity, we have

$$N_e = N'_e\left(1 - \frac{F}{2M}\right) \tag{12}$$

which predicts long-term equilibrium abundance in the presence of removal rate F. In parallel with our treatment of short-term impact, the long-term equilibrium abundance of a harvested or impacted stock relative to the abundance of the virgin stock is denoted R_e, and is given by

$$R_e = N_e/N'_e \tag{13}$$

and according to Equation (12), we have the approximation

$$R_e = \left(1 - \frac{F}{2M}\right). \tag{14}$$

Equation (14) says that we can estimate the impact of all removals, given the total rate of removals and the rate of adult natural mortality.

The total rate of removals (F) includes entrainment (E) and impingement (F_p) by all power plants operating in the area of the stock, and all fisheries (F_f) exploiting the stock:

$$F = \Sigma E + \Sigma E_p + \Sigma F_f. \tag{15}$$

The removal rate due to entrainment (E) is estimated by the method presented in the previous section, i.e.,

$$E = \Sigma E_i t_i. \tag{16}$$

Impingement (F_p) and fishing (F_f) mortality rates may be estimated by a method similar to Equation (7):

$$F_p = I/\bar{N}^* \tag{17}$$

and

$$F_f = C/\bar{N}^* \tag{18}$$

where I is the number of adults impinged in a year, C is the annual fishery harvest, and $\bar{N}^*$ is the mean abundance of the stock over the year.

The natural mortality rate is a difficult parameter to estimate. Ricker (1975) reviewed many of the methods. In some cases it may be necessary to assume a value of M, based on comparison with better known species. One useful method, based on comparative growth and environmental parameters, has been described by Pauly (1980). If a mortality rate can be es-

timated, for example, based on age frequency, the estimate will often be the total mortality rate of adults (Z), where

$$Z = M + \Sigma F_p + \Sigma F_f. \quad (19)$$

The natural mortality rate can be obtained from

$$M = Z - \Sigma F_p - \Sigma F_f. \quad (20)$$

If fish are being removed from the stock by several power plants and fisheries, the impact by a single entity cannot be considered in isolation. Our proposed method of long-term impact assessment allows an integrated assessment of impact, but also allows dissection into individual contributions to the total impact. Equation (15) states that the total rate of removals (F) is the sum of the individual instantaneous rates of removal. Since Equation (15) is a linear function, the fraction of the total impact which is attributable to any particular entity is the ratio of the sum of its contributions to total F from all sources as in Equation (15).

CRITERIA FOR IMPACT EVALUATION

Removal of fish from a stock, whether by a fishery or by a power plant, will usually lead to lowered equilibrium abundance. The previous section has presented a method for estimating the approximate reduction in abundance which has taken place. We must now determine whether this impact is "acceptable." In the case of a fishery where tangible values can be assigned to the catch and the stock, optimal catch rates and population sizes can be defined (Roedel 1975; Clark 1976). However, losses to a power plant produce no direct consumptive benefit, and, in many cases, the impacted stock is not subject to a fishery and therefore has no conventional value.

Fortunately, there exists a precedent for evaluating impacts on nonvalued species. The Marine Mammal Protection Act, enacted by the United States in 1972, requires that marine mammals be managed for optimum sustainable population size (OSP). Subsequently, the term was given a working definition: "Optimum sustainable population is a population size which falls within a range from the population level of a given species or stock which is the largest supportable within the ecosystem to the population level that results in maximum net productivity. Maximum net productivity is the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality." (Gehringer 1976).

While power plants clearly do not directly impact marine mammals, the principle of optimum sustainable population size as defined above may be extended to fish and invertebrates as well. Since OSP is defined to fall within a range, impact is unacceptable when it causes population size to fall below the lower limit of that range, which is the point of maximum net productivity. In the logistic model assumed by our long-term impact assessment, maximum net productivity occurs at one-half the virgin, unimpacted population size. This gives a simple criterion for acceptable impact: Abundance should not be driven below one-half of its unimpacted level. In terms of the long-term impact model and its assumptions, this criterion is equivalent to saying that the rate of removal should not exceed the adult rate of natural mortality.

EXAMPLE APPLICATION

This example is based on data collected during 1978 for the purpose of estimating power plant impact on topsmelt, *Atherinops affinis*, inhabiting a California estuary.[4] Topsmelt is a bay-dwelling species with demersal eggs and a short (2-3 mo) spawning period. Topsmelt eggs hatch to produce 6 mm larvae, and larvae >15 mm are not entrained. Larvae were categorized by two length stages, 6-10 mm and 11-15 mm. Based on laboratory growth rate experiments for a closely related atherinid, the California grunion, *Leuresthes tenuis*, duration of these two stages is about 14 d each.

Standing stock and entrainment data (Table 1) are averages for the 3-mo spawning period based on biweekly sampling. Since larvae are concentrated near the surface during daylight hours, larval standing stock estimates are determined based on daytime surface larval densities sampled by a neuston net. These density values are extrapolated to the area of the estuary and a depth of 1 m. The mean entrainment rates are adjusted for variation in cooling water flow during each of the sampling periods. All entrained larvae are assumed to die. The short-term impact of the power plant is estimated to reduce recruitment strengths to 98% of their unimpacted value. Based on seine catches, the standing stock of adult topsmelt in the estuary was 5.4×10^5 fish. Since the power plant has long been operational, equi-

[4]Because the power plant impact study has not completed the official review process, the proprietor wishes not to be identified at this preliminary stage.

TABLE 1.—Example calculation of short-term impact by entrainment of topsmelt larvae. n.e. indicates not estimated.

Stage	Entrainment (L_i) larvae/day	Standing stock (L_i^*) larvae	Entrainment rate (E_i) per day	Stage duration (t_i) days	$E_i t_i$
Eggs	0	n.e.	n.e.	n.e.	0
Larvae					
6-10 mm	4.0×10^4	5.3×10^7	7.5×10^{-4}	14	1.1×10^{-2}
11-15 mm	2.0×10^3	3.0×10^6	6.7×10^{-4}	14	0.9×10^{-2}
16 + mm	0	n.e.	n.e.	n.e.	0
Sum					2.0×10^{-2}

Equation (5): $R_c = \exp(-2.0 \times 10^{-2}) = 0.98$.
Equation (11): $A_e = 5.4 \times 10^5 (0.98^{-1} - 1) = 1.1 \times 10^4$ fish.

valent adult losses are estimated by Equation (11) and are 1.1×10^4 fish.

Estimation of long-term impact requires information on all sources of mortality. The annual estimate of adult impingement by the power plant, based on 360 d of sampling, is 5,147 fish. According to California Department of Fish and Game records, there were no commercial landings of topsmelt in 1978, and recreational fishermen landed <1,000 topsmelt in this area (we use 1,000 fish for this example). Total mortality rate was estimated by regressing log abundance against age (Ricker 1975), giving an instantaneous total mortality rate (Z) of 1.8. Nonnatural mortality rates of adults were negligible (Table 2), giving a natural mortality rate of $M = 1.8$. Application of the long-term impact approximation (Equation (14)) indicates that topsmelt may be near 99% of their unimpacted abundance despite impacts by both power plants and fisheries. The majority of impact on the local resource is probably due to power plant operation, with entrainment impact being about twice as large as impingement impact. In any case, this estimated small reduction in long-term abundance indicates that there is no cause for concern with regard to power plant impact on topsmelt abundance in this estuary.

TABLE 2.—Example calculation of long-term impact from all sources of topsmelt mortality.

Source of impact	Catch (fish)	Mean standing stock (fish)	Coefficient of mortality
Impingement	5,147	5.4×10^5	1.0×10^{-2} (F_p)
Fishery	1,000	5.4×10^5	0.2×10^{-2} (F_f)
Entrainment	(see Table 1)		2.0×10^{-2} ($\Sigma E_i t_i$)
Sum			3.2×10^{-2}

Equation (20): $M = 1.8 - 1.0 \times 10^{-2} - 0.2 \times 10^{-2} = 1.8$.
Equation (14): $R_e = 1 - (3.2 \times 10^{-2}/3.6) = 0.99$.

DISCUSSION

This approximation of long-term impact is not intended to be a substitute for proper studies of population dynamics. Rather, just as in the case of fishery management, it is intended to be a working approximation which should be discarded as more definitive information and analyses become available. In the case of impact assessment there will always be a suite of organisms, particularly invertebrates, which undoubtedly are impacted, but lack sufficient "status" to justify the expense of close monitoring and study. For these organisms, approximation is the most that reasonably can be asked. In this respect the potential yield approximation is well established in fishery management and should therefore be an equally applicable approximation for power plant impact assessment.

It is likely that the bases of the approximation can be improved in two ways. First, organisms may be classifiable into types with various productivity curves, of which the logistic is a special case. For example, Fowler (1981) observed that species with high reproductive rates and short life-spans show most density-dependent compensation at low population levels, whereas species with low reproductive rates and long life-spans show most of their density-dependent compensation near carrying capacity. Thus, it may be possible to specify the shape of the curves in Figure 1 as a function of observable or measurable traits of specific organisms. The second improvement consists of developing better scaling criteria for the production curve, once its shape has been established. A survey of population growth rates of many species could form the basis of an empirical estimator of compensatory capacity; the use of natural mortality rate may not be appropriate in many cases. Clearly, an improved approximation method would be of value both to fishery management and to power plant impact assessment.

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NOTES

THE SIZE AT SEXUAL MATURITY OF BLUE KING CRAB, *PARALITHODES PLATYPUS*, IN ALASKA[1]

The blue king crab, *Paralithodes platypus*, is similar in size and general morphology to the better known and commercially more important red king crab, *P. camtschatica*. Unlike the red king crab, which is generally distributed throughout most of coastal Alaska, the blue king crab only occurs in small isolated populations. The principal fisheries for blue king crab occur in the eastern Bering Sea, where most populations are associated with offshore islands; minor, but locally important, fisheries occur south of the Alaska Peninsula, where populations are found in a number of widely scattered, enclosed bays.

Harvest of both species of king crab is restricted to males larger than minimum size. For red king crab, the minimum size is set at the average size of a male 3 yr after reaching sexual maturity in an attempt to assure that each male will have at least one opportunity to mate before becoming available for harvest (North Pacific Fishery Management Council 1981). For blue king crab, however, the size at maturity is not well known, and in some areas the minimum size limit is set at the same size as red king crab.

In this paper we estimate the size at maturity of female and male blue king crab in each of four populations. For females, the size at sexual maturity is based on the change in the presence of eggs or egg remnants on the pleopod setae as a function of size. For males, the size at maturity is based on chela allometry, using a new computer technique to estimate the size at which chela growth increases relative to carapace growth.

Materials and Methods of Collection

Samples of blue king crab were collected from each of four populations: St. Matthew Island, Pribilof Islands, Olga Bay, and Prince William Sound (Fig. 1). Sampling methods differed somewhat between populations. The populations from St. Matthew Island and Pribilof Islands were sampled with bottom trawls on cruises conducted by the National Marine Fisheries Service during the months of June and July of each year from 1976 to 1981. Sampling depths ranged from 30 to 180 m. The Olga Bay population was sampled by scuba divers and with hand operated ring nets in March, June, and October 1980 and January 1981. Sampling depths ranged from 1 to 50 m. The Prince William Sound population was sampled with bottom trawls in September 1980 and with commercial king crab pots in September 1979 and December 1980. Sampling depths ranged from 80 to 150 m.

Carapace length of both sexes and the major (righthand) chela height of males were measured to the nearest 1 mm using sliding jaw calipers (see Wallace et al. 1949 for definitions of these measurements). Reproductive condition of females was classified as either

virgin—no eggs or egg remnants attached to the pleopod setae,
attached eggs—eggs attached to the pleopods, or
hatched eggs—egg remnants, consisting of egg membranes and egg funiculi, attached to the pleopod setae.

Female Size at Maturity

Female blue king crab mate and extrude eggs quite soon after every adult molt (a pathological exception to this is discussed in Somerton and MacIntosh[2]); therefore, females can be classified as mature or immature based on the presence or absence of eggs or egg remnants on the pleopods. Using this classification criterion, the percent of females that were mature was calculated for each 3 mm size interval. Percent mature is plotted against carapace length in Figure 2.

The size at 50% maturity (SM50) was chosen as an appropriate measure of the size at maturity [see Somerton (1981) for a discussion of the strengths and weaknesses of this particular measure]. SM50 was estimated for each population by fitting a logistic equation to percent mature by size, using weighted nonlinear least squares (Somerton 1980a), then

[1]Contribution No. 625, College of Fisheries, University of Washington, Seattle, WA 98195.

[2]Somerton, D. A., and R. A. MacIntosh. In prep. Reproductive biology of the blue king crab, *Paralithodes platypus*. Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle, WA 98195.

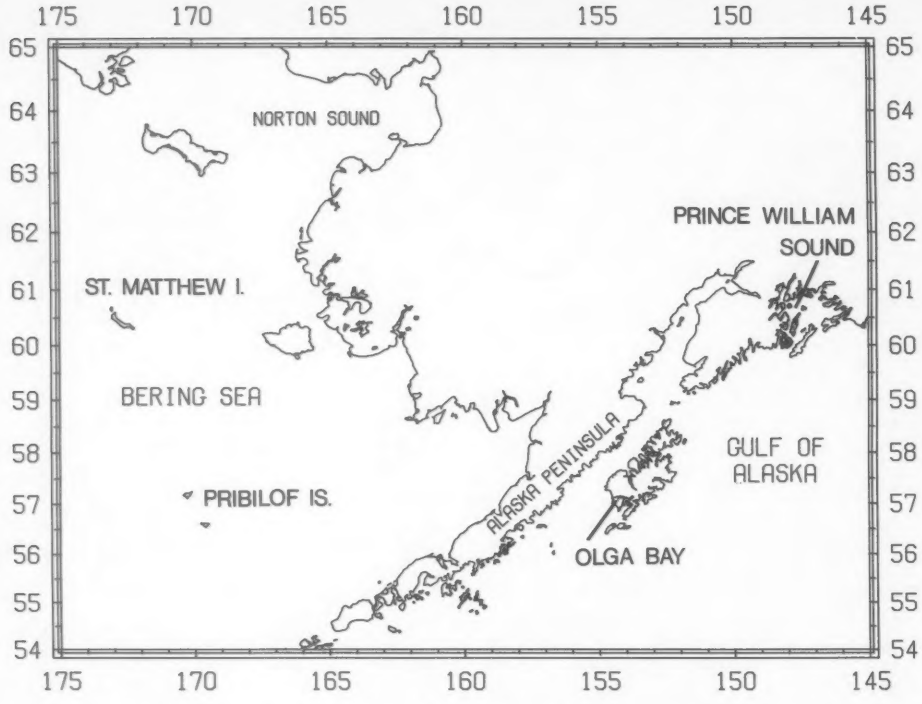

FIGURE 1.—Locations of the four blue king crab populations: St. Matthew Island, Pribilof Islands, Olga Bay, and Prince William Sound.

evaluating the fitted equation to find the size corresponding to 50% maturity. Variance of SM50 was estimated using the technique described in Somerton (1980a). Estimates of SM50, standard deviations, and 95% confidence intervals are shown in Table 1.

TABLE 1.—Female size at 50% maturity (SM50), standard deviation, and 95% confidence intervals for each of the four blue king crab populations studied.

Area	SM50 (mm)	Standard deviation	95% confidence interval
St. Matthew Island	80.6	0.6	79.4-82.6
Pribilof Islands	96.3	0.3	95.7-96.9
Olga Bay	93.7	0.4	92.9-94.5
Prince William Sound	87.4	0.5	86.4-88.4

Male Size at Maturity

Male blue king crab do not display external features that unambiguously indicate maturity; however, at maturity the growth of the major chela may increase relative to the growth of the carapace. Although this relationship has not been established for blue king crab, for tanner crab, *Chionoecetes bairdi*, the size of maturity based on chela allometry was almost identical to that based on a change in reproductive tract weights (Brown and Powell 1972). If this is also true for blue king crab, then the size at maturity can be estimated by the size at which chela growth increases.

When chela measurements are plotted against carapace measurements on log-log axes, the data assume a pattern consisting of two straight lines. These lines describe the juvenile and adult phases of relative growth (Hartnoll 1978). For some species of crab, especially brachyuran crabs, the two lines have similar slopes but different intercepts. Somerton (1980a) described a technique for estimating the size of maturity for species with this pattern of relative growth. For other species, including blue king crab, the two lines have different slopes and intersect at the size at maturity. In this case, the problem of estimating the size at maturity is one of estimating the intersection point of the two phase lines.

The intersection point can be estimated from morphometric data by finding the best fit of a model

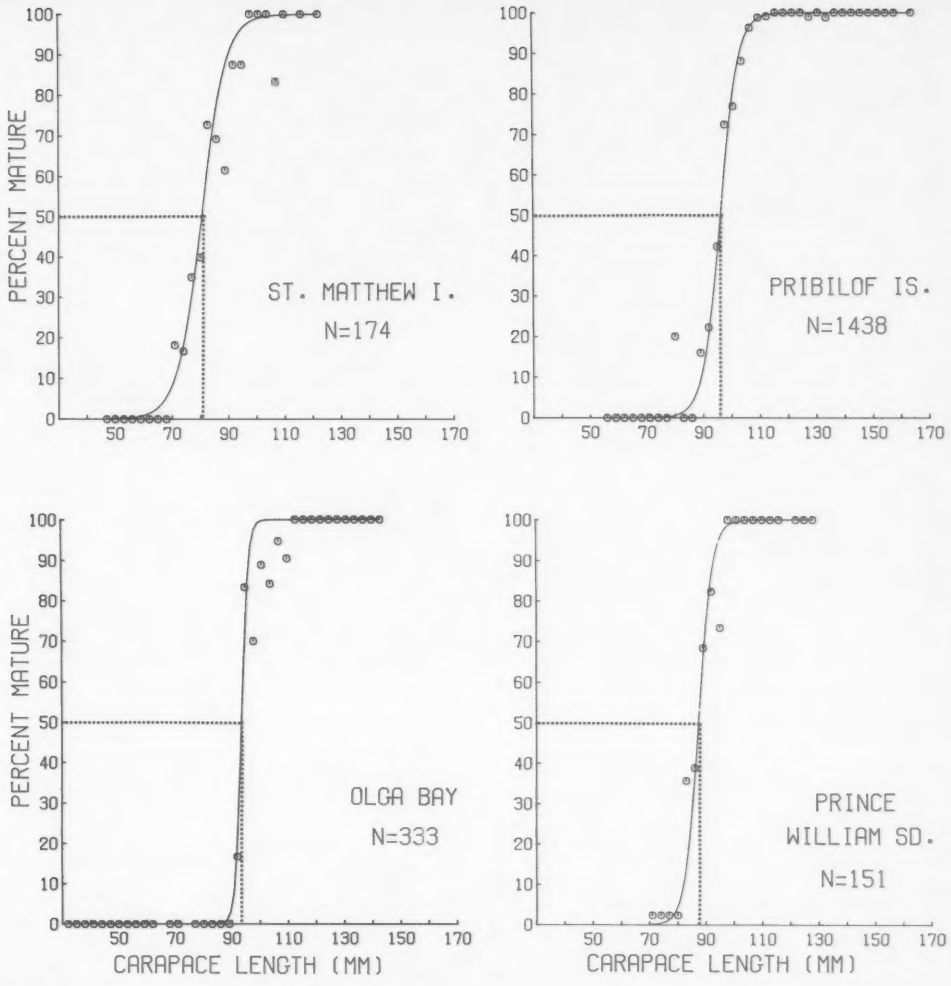

FIGURE 2.—Percent of blue king crab females that were mature, within 3 mm size intervals, as a function of size. Dotted lines indicate the carapace lengths corresponding to the 50% maturity levels on the fitted logistic functions (solid lines). Sample sizes (N) are indicated.

which describes a pair of intersecting straight lines and has the intersection point as a parameter. One such model, which has been previously used (Somerton 1980b) to describe the relation between premolt and postmolt carapace size, is

$$Y = A + BX \qquad X \leq X^*$$
$$Y = Y^* + C(X - X^*) \qquad X > X^*$$

where Y and X are the logarithms of chela height and carapace length, X^* is the intersection point on the X axis, and Y^* is the intersection point on the Y axis, ($Y^* = A + BX^*$). The model has four parameters. A, B, C, and X^*.

This model was fit to morphometric data using an iterative computer technique (FORTRAN program MATURE2 is available from the senior author). First, a lower and an upper bound of an interval on the X axis are chosen such that the intersection point is contained within the interval. Second, X^* is set

equal to the lower bound and linear regression is used to fit a lower line ($X \leq X^*$), then an upper line ($X > X^*$) to the data. Third, X^* is increased by some small amount and the model is fit to the data iteratively until X^* equals the upper bound. The size of sexual maturity is then equal to the antilog of the X^* value, which produced the minimum residual sum of squares about the model. Chela and carapace measurements and the best fitting pair of lines are shown in Figure 3.

Although this technique will always find the best fit of the model, the fit may not be statistically significant, that is, the fit of the two line model may not be significantly better than the fit of a single straight line. Therefore a single straight line was fit to the data and the residual sum of squares (RSS) of the two line model was tested against the RSS from the single line using a partial F test (Draper and Smith 1981). The partial F test was significant ($P<0.05$) for all four sets of blue king crab data. In cases where the fit of the two

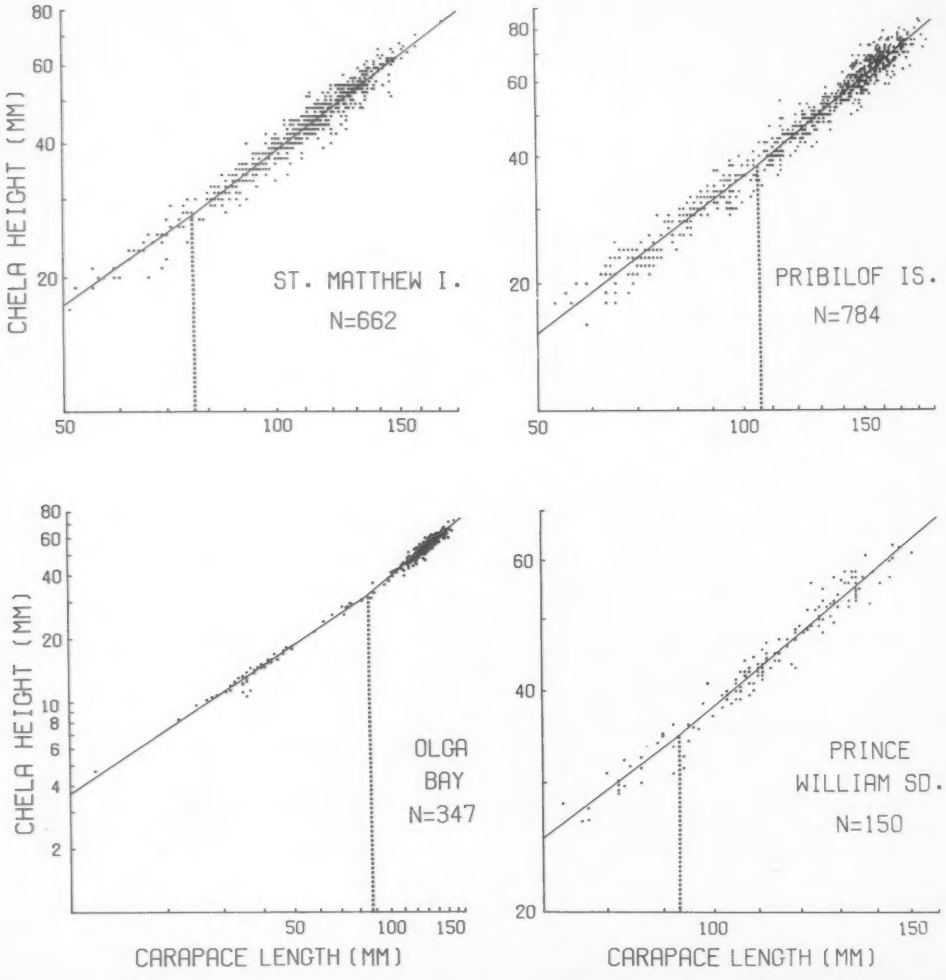

FIGURE 3.—Male chela heights and carapace lengths of the blue king crabs. The X axis intersection points of the two line model, or the estimated sizes of maturity, are shown by dotted lines. Sample sizes (N) are indicated.

line model is not significantly better than the fit of a single line, either more data or a broader size range of data is needed or some other procedure for estimating the size of maturity should be considered.

The standard deviation of X^* was estimated using Monte Carlo simulation (Hammersley and Handscomb 1964), which, in this particular application, consisted of 1) generating sets of synthetic morphometric data, 2) estimating X^* for each data set by fitting the two line model, and 3) calculating the standard deviation between the estimates of X^*. Each synthetic data set was constructed by generating a new chela measurement for each carapace measurement in the original sample. The new chela measurement was computed as

$$Y = E(Y) + Z \cdot SD$$

where Y is the logarithm of chela height, $E(Y)$ is the expected value of log chela height given carapace length and the parameters of the appropriate phase line, Z is a randomly generated standard normal deviate, and SD is the standard deviation about the appropriate phase line. For carapace widths $\leq X^*$, the parameters and SD for the juvenile phase line were used; for carapace widths $> X^*$, the parameters and SD for the adult phase line were used. Thirty samples of morphometric data were generated for each population. X^* was estimated for each sample and the standard deviation among the 30 independent estimates of X^* was calculated. The estimates of X^*, standard deviations, and 95% confidence intervals are shown in Table 2.

Samples from the populations of St. Matthew Island and Pribilof Islands contained some chela measurements that were unusually small compared with other measurements from crabs with similar carapace lengths (Fig. 4). These atypical measurements were probably obtained from crabs in the process of regenerating lost chelipeds. For crabs which are bilaterally symmetric, the inadvertent measurement of partially regenerated chelae should not be a problem, because the sizes of left and right chelae can be compared in the field, and, if different, the measurement can be rejected. For crabs, such as blue king crab, which are not bilaterally symmetric, partially regenerated chelae are harder to detect and thus are likely to be included in the sample. For red king crab, the

TABLE 2.—Male size at maturity, standard deviation, and 95% confidence intervals for each of the four blue king crab populations studied.

Area	Size at maturity (mm)	Standard deviation	95% confidence interval
St. Matthew Island	77.0	9.8	57.8-96.2
Pribilof Islands	108.0	12.8	82.9-133.1
Olga Bay	87.0	7.2	72.9-101.1
Prince William Sound	93.0	13.9	65.7-120.2

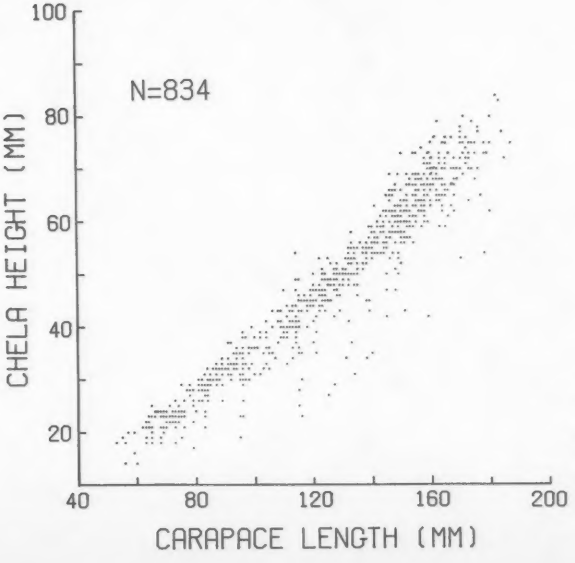

FIGURE 4.—Male chela height and carapace length measurements of the blue king crab from the Pribilof Islands before date deletion. Measurements of chela height which appear unusually small relative to the carapace length probably were obtained from crabs in the process of regenerating lost chela.

length of a limb after each of the five molts required for complete regeneration is 27, 45, 65, 85, and 100% of the length of a normal limb (Edwards 1972). Limbs in the last stages of regeneration are the hardest to detect.

Since measurements from regenerating chelae can be quite deviant from normal measurements, they can have a pronounced effect on the estimate of X^* and therefore must be detected and eliminated from the sample. The method we used for eliminating such outliers consisted of fitting a single straight line to the logarithms of chela height and carapace length (fitting the two line model is preferable if computer cost is not a consideration) then excluding the datum with the largest negative deviation. This is repeated iteratively until the mean square residual (MSR) is reduced to some level.

Two criteria were examined as a means of determining when MSR had been reduced sufficiently. The first criterion considered the change in MSR resulting from the deletion of each successive datum. Typically the change in MSR was initially large, then decreased almost asymptotically as additional data were deleted (Fig. 5). Elimination of regenerating chela measurements was assumed to be complete when the change in MSR became nearly constant. For the Pribilof Islands population, data deletion was halted after 50 values (6% of the sample) were removed (Fig. 6).

The second criterion was based on a comparison of the MSR of the contaminated sample with the MSR of a sample assumed to be free of regenerating chela measurements. Deletion was halted when the MSR of the contaminated sample was not significantly different from the uncontaminated sample, based on an F ratio, at some probability level. Although this criterion is more objective than the first, it requires an uncontaminated sample and it assumes that the true variance is identical between populations. For the Pribilof Islands data, to achieve an MSR that was not significantly different from the average MSR for the Olga Bay and Prince William Sound data (both of these data sets did not contain regenerating chelae measurements) at the 0.001 probability level, 114 values (14% of the sample) had to be excluded (Fig. 7). Even with this low probability level, the deletion of data was too severe, because the distribution of chela measurements about the fitted line appeared to have a positive skew. Since we believe that the true variance is probably less in the Olga Bay and Prince William Sound populations than in the Pribilof Islands population, the first criterion was used to determine when the deletion of data should be halted.

The number of data deleted by these methods may be too large, that is, some crabs with small, but otherwise normal, chela may have been excluded. In one study of limb regeneration in male red king crab, 14.7% of the adults and 25.6% of the juveniles had

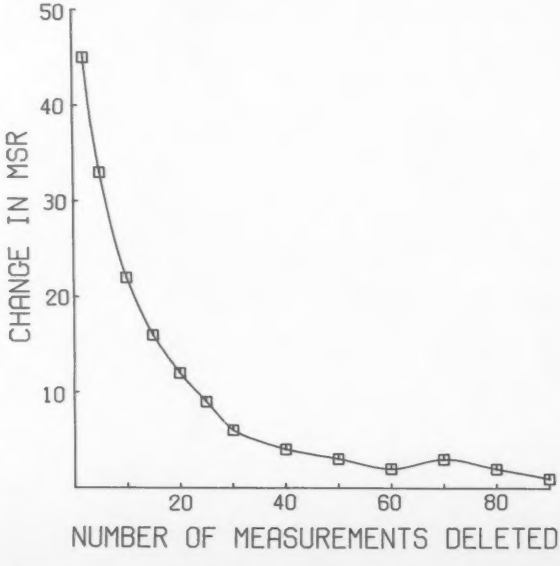

FIGURE 5.—Change in mean square error (MSR) about a single straight line fit to the data of the blue king crab from the Pribilof Islands as a function of the number of values deleted. Note that the change in MSR becomes nearly constant after deleting 50 values.

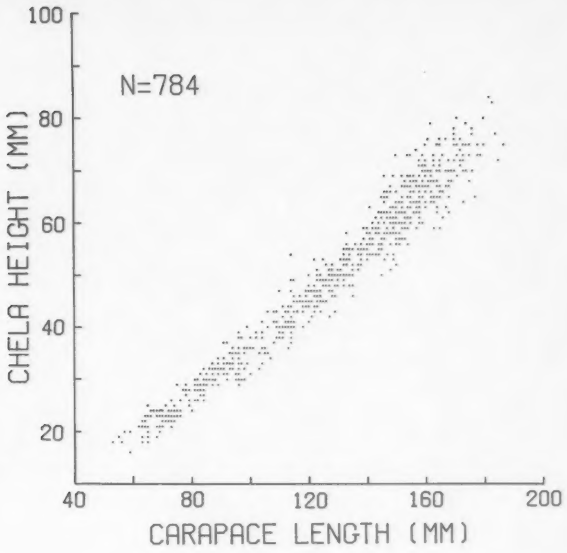

FIGURE 6.—Chela height and carapace length data of the blue king crab from the Pribilof Islands after the deletion of 50 values.

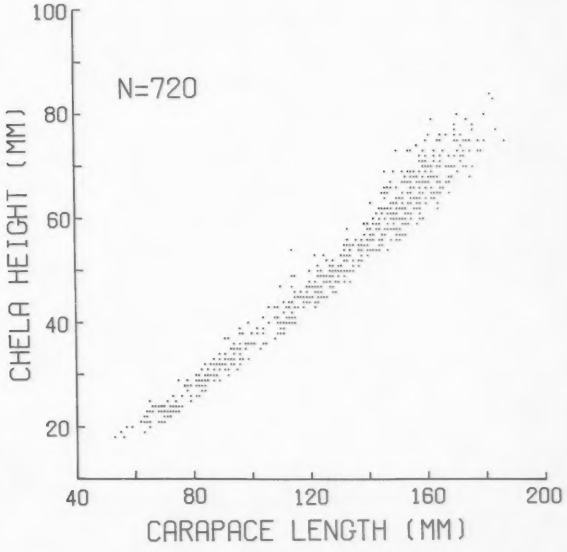

FIGURE 7.—Chela height and carapace length data of the blue king crab from the Pribilof Islands after the deletion of 114 values.

missing or regenerating limbs and 8.4% of the missing or regenerating limbs were the right cheliped (Edwards 1972). Thus 1.2% of all adult males and 2.2% of all juvenile males had missing or regenerating right chela. For the Pribilof Islands sample, 6.0% of the total sample was deleted. Although some valid measurements may have been rejected, the loss of these measurements should bias the estimate of X^* less

than the inclusion of measurements from regenerating chela.

Results and Discussion

For both sexes of blue king crab, estimates of the size at sexual maturity were largest at Pribilof Islands, smallest at St. Matthew Island, and intermediate between these extremes at Olga Bay and Prince William Sound (Tables 1, 2). Precision in the estimates of the size at maturity of blue king crab differs markedly between sexes. For females, the average standard deviation was 0.45 mm, whereas, for males, the average standard deviation was 10.93 mm, about 24 times larger. Because of this difference, the estimates for females differed significantly (Z test, $P<0.5$) between all areas, but the estimates for males did not differ between areas even though their range was nearly double that of females.

Much of the imprecision in the estimates of male size at maturity is the result of the pattern of relative growth. Standard deviation of an estimate of male size at maturity depends largely on the angle at which the two phase lines meet. As the included angle increases, uncertainty in the position of each phase line is progressively magnified in the uncertainty of the estimate of the size of maturity. Species, such as blue king crab, which exhibit a large angle between phase lines, inherently have a large standard deviation.

Future studies of male crabs with a similar pattern of relative growth should insure that samples include a broad range of sizes, because this will minimize the standard deviation of the estimates of size at maturity. The relationship between size range and standard deviation is exemplified by the two extreme cases examined here. The Olga Bay sample, which produced the smallest standard deviation, included individuals as small as 12 mm, whereas the Prince William Sound sample, which produced the largest standard deviation, included no individuals smaller than 72 mm.

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FOOD HABITS OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*, OFF THE WEST COAST OF NORTH AMERICA, 1967 AND 1980

The Pacific whiting, *Merluccius productus*, forms a major groundfish resource off the west coast of North America. According to Nelson and Larkins (1970) it is "one of the most abundant species of fish in the northeastern Pacific Ocean." Fishing effort on the Pacific whiting stock has increased dramatically since 1965 when it became the target of the United States and Soviet fishermen (Grinols and Tillman 1970). The stock is now the basis of a large U.S. joint-venture and domestic fishery. Management of this stock requires more detailed information on the major prey of Pacific whiting throughout its distribution.

Previous studies have shown that Pacific whiting feed primarily on euphausiids, but at certain times commercially important fish or pandalid shrimp may constitute an important item in the diet (Gotshall 1969a, b; Alton and Nelson 1970; Outram and Haegele 1972). Indirect evidence of nocturnal feeding by Pacific whiting has also been presented by Alton and Nelson (1970) and by Outram and Haegele (1972). Although these studies contain useful baseline information, they are not complete enough to describe quantitatively the predatory interactions of Pacific whiting, with the exception of Gotshall's (1969a, b) study which focused only on the impact of whiting predation on the commercially important pink shrimp, *Pandalus jordani*.

The objective of the present study is to provide a quantitative account of the predatory patterns of Pacific whiting by identifying their major prey items, determining whether size-selective predation occurs, examining diel feeding behavior, and calculating daily ration.

Collection and Processing of Samples

Stomachs of adult Pacific whiting were collected in 1967 off the Oregon and Washington coasts (Livingston and Alton 1982) and in 1980 off Oregon, Washington, and Vancouver Island (Fig. 1). Also, samples of juvenile Pacific whiting taken off the California coast in the fall of 1980 were saved for stomach analysis (Table 1). Samples were obtained during resource assessment surveys using either bottom or midwater trawls. Only vessels operating during daylight hours used bottom trawls to survey whiting which were mostly on the sea bottom. Midwater trawls were used on those vessels with both day and night operations so that the net could be set at depths of greatest whiting concentration. Stomach samples were taken opportunistically at standard resource assessment stations. In 1967, most stations were at bottom depths of <100 m, while in 1980 bottom depths ranged from 77 to 298 m. Stomachs were taken randomly from the entire catch in 1967, but were stratified in 1980 by 10 cm whiting length groups.

A 15-h time series of stomach samples was taken in 1967 at a station off the Washington coast to detect

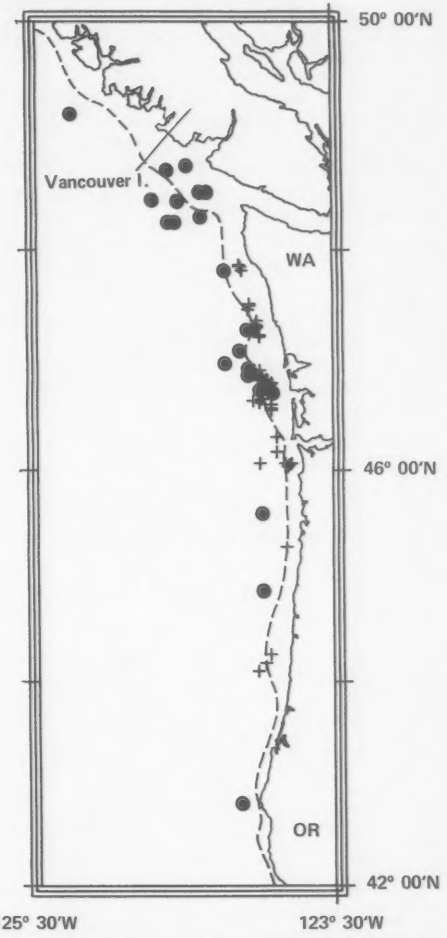

FIGURE 1.—Sampling locations for Pacific whiting, *Merluccius productus*, in 1967 (+) and 1980 (·) in relation to the 100 m depth contour (---).

TABLE 1.—Dates, locations, station information, and sample sizes of stomach samples of Pacific whiting taken from the northwest Pacific Ocean, 1967 and 1980.

Vessel	Location	Sampling period	Tows		Bottom depth range (m)	No. of stomachs collected[3]
			Number[1]	Type[2]		
RV *John M. Cobb*	Oregon	Apr.-July 1967	6 (2)	MW	84-126	104 (86)
RV *Commando*	Oregon	June 1967	1 (1)	MW	144	7 (8)
MV *Baron*	Oregon	June 1967	4 (0)	MW	49-77	91 (5)
RV *John M. Cobb*	Washington	May-July 1967	30 (2)	MW	53-156	785(108)
MV *Baron*	Washington	June 1967	8 (0)	MW	62-75	191 (56)
MV *Recruit*	Washington	June 1967	1 (0)	MW	75	9 (2)
MV *St. Michael*	Washington	June-July 1967	9 (0)	MW	55-84	243 (54)
RV *Tikhookeanskiy*	Oregon	Apr.-May 1980	3 (3)	BT	120-200	53 (13)
RV *Miller Freeman*	Washington-Vancouver I., B.C.	Aug.-Sept. 1980	6 (6)	MW	111-298	34 (–)
MV *Pat San Marie*	Washington-Vancouver I., B.C.	Sept. 1980	14(10)	BT	77-293	77 (–)
RV *Poseydon*	California	Oct. 1980	2 (2)	BT	130-160	40 (12)

[1]Number of tows at bottom depths >100 m are given in parentheses.
[2]MW = midwater trawl; BT = bottom trawl.
[3]Stomachs containing food. Number of empties in parentheses.

feeding discontinuity. A total of 258 stomachs were collected at seven different times of day (Table 2).

Fish showing signs of regurgitation were discarded from samples. Lengths were recorded for fish with stomachs containing food. The stomachs of adult fish were then excised and placed in muslin bags with a specimen card containing fish length and station information. Juvenile fish were placed whole in muslin bags for later stomach excision in the laboratory. All samples were preserved in a 10:1 seawater/formaldehyde mixture.

Because of incomplete records of numbers of empty stomachs sampled on two cruises in 1980, that data set could not be used for daily ration calculations. In 1967, however, numbers of empty stomachs at each station were recorded along with corresponding fish lengths.

Fish lengths were converted to weights using the weight-length relationship for Pacific whiting, sexes combined (Traynor[1]):

$$w_g = 0.004774 \; l_{cm}^{3.0947}.$$

[1]J. Traynor, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, pers. commun. December 1982.

TABLE 2.—Summary of a diel series of Pacific whiting stomach samples obtained on RV *John M. Cobb*, 14-15 July, 1967 off the Washington coast lat. 47° 19'N, long. 124° 33'W at a bottom depth of 65 m.

Time of day (P.S.T.)	No. of stomachs		Total weight of stomach contents (g)	Mean fish length (mm)
	With food	Empty		
1800	30	1	557.9	486
2100	34	2	474.8	429
2300	36	0	215.6	509
0100	61	1	348.2	524
0300	35	1	373.8	500
0400	17	2	83.9	533
0900	38	0	403.3	484
	251	7		

Stomachs were analyzed individually in the laboratory, with the exception of the fall 1980 samples which were analyzed by composite groups. Prey items were identified to the lowest practical taxon, and damp weight and number of each prey taxon per stomach or composite of stomachs were recorded. In 1967, there was some loss of information on the number of prey in some taxa because no attempt was made to count certain prey items when they showed a fair degree of digestion.

Food of Pacific Whiting

Euphausiids, including *Thysanoessa spinifera* and *Euphausia pacifica*, were the dominant food of Pacific whiting in 1967, constituting 72.2 and 90.2% by weight of the diet of Pacific whiting taken off Oregon and Washington, respectively (Table 3). In 1980, euphausiids were also the predominant item in the diets of Pacific whiting <200 mm in length off California (100% by weight) and of Pacific whiting 350-449 mm long off Oregon (99.6% by weight).

Schooling fish were also important dietary components for Pacific whiting. Northern anchovy, *Engraulis mordax*, comprised 16.4% by weight of the diet of Pacific whiting in summer 1967 off Oregon. In spring 1980 off Oregon, eulachon, *Thaleichthys pacificus*, comprised 22% by weight of the diet of 450-549 mm Pacific whiting and 79.6% by weight of the diet of 550+ mm fish. Pacific herring, *Clupea harengus pallasi*, dominated the diets of Pacific whiting taken in summer 1980 off Washington and Vancouver Island, constituting 54.2 and 67% by weight of the 450-549 mm and 550+ mm whiting size groups, respectively.

Other fish items were predominantly flatfish and rockfish, *Sebastes* sp. Pandalid shrimp, including *Pandalus jordani*, comprised <5% by weight of the

TABLE 3.—Percentage by weight of prey items in the stomachs of Pacific whiting, 1967 and 1980, off the west coast of North America and summary of average stomach content weight (not including empty stomachs)[1].

	Summer 1967		Fall 1980	Spring 1980			Summer 1980	
	Oregon	Washington	California	Oregon			Wash.-Vancouver I.	
	Mean predator size (mm)		Predator-size group (mm)					
Prey item	491	503	<200	350-449	450-549	550+	450-549	550+
Crustacea								
Euphausiids								
T. spinifera	21.1	35.3	72.5	6.2	9.1	T	19.0	1.7
E. pacifica	1.7	0.3	6.8	93.0	26.9	1.0	4.2	3.0
Unidentified	49.4	54.6	20.7	0.4	23.4	0.2	6.6	2.7
Crab megalops larvae	1.1	0.1						
Mysidacea	T	T	T	—	—	—	—	T
Pandalidae (unidentified)	0.3	0.3	—	—	3.7	4.5	3.0	0.3
Pandalus jordani	—	—	—	—	—	—	0.7	1.7
Sergestes similis	—	T	—	—	—	—	0.1	0.2
Pasiphaea pacifica	—	—	—	—	—	—	—	0.1
Spirontocaris sp.	—	—	—	—	—	—	—	T
Crangon sp.	0.2	0.2	—	—	—	—	0.4	—
Caridea (unidentified)	0.1	0.4	—	—	—	—	0.1	—
Gonatus sp.	—	—	T	—	0.1	0.2	—	—
Pisces								
Engraulis mordax	16.4	0.1	—	—	—	—	—	—
Clupea harengus	—	—	—	—	—	—	54.2	67.0
Thaleichthys pacificus	—	—	—	—	22.0	79.6	3.3	9.4
Osmeridae	0.7	0.8	—	—	7.8	—	1.0	2.3
Sebastes sp.	—	T	—	—	—	—	4.1	0.1
Liparis fucensis (larvae)	—	—	—	—	—	—	0.2	—
Agonidae	—	—	—	—	—	—	0.5	—
Gadidae	—	1.3	—	—	—	—	0.2	—
Pleuronectidae (unid.)	—	T	—	—	6.8	6.3	0.6	—
Citharichthys sp.	—	—	—	—	—	—	0.6	—
Poroclinus rothrocki	—	—	—	—	—	—	0.7	—
Icicthys lockingtoni	—	—	—	—	—	—	—	8.9
Zoarcidae	—	0.5						
Unidentified	8.8	5.7	—	0.4	0.2	8.1	0.5	2.5
Number of Stomachs	202	1,228	40	16	17	20	70	41
Total weight of stomach contents(g)	2,403.8	10,560.8	13.65	133.7	86.74	607.3	849.1	934.6
Mean stomach content weight (g)	11.9	8.6	3.3	8.4	5.1	30.4	12.1	22.8
Mean fish length (mm)	491	503	132	380	506	587	529	591
Percentage body weight of stomach contents	1.46	0.96	23.57	2.27	0.57	2.14	1.18	1.57

[1]T indicates trace amounts of food, i.e. <0.1% by weight of the diet.

Pacific whiting diet in all cases. Other shrimp eaten included *Cragon* sp., *Pasiphaea pacifica*, and *Sergestes similis*. Other invertebrates were predominantly crab megalops larvae.

In terms of general prey categories, Pacific whiting in 1967 off Oregon ate proportionally more fish, especially northern anchovy, than did whiting in 1967 off Washington (Fig. 2). The diets of similar-sized Pacific whiting (450-549 mm) taken in 1980 off Oregon and Washington-Vancouver Island, however, contained an even greater proportion of fish (Fig. 3), but of different species. A shift in major dietary component from euphausiids to fish occurred as the length of Pacific whiting increased during spring and late summer of 1980. Diets of Pacific whiting >550 mm consisted of 90.2% fish by weight.

To illustrate the switch in food from euphausiids to fish as the length of Pacific whiting increased, the percentage frequency of occurrence of Pacific herring in Pacific whiting stomachs was plotted against Pacific whiting length for the late summer 1980 samples (Fig. 4). A steady increase in the occurrence of Pacific herring is noticeable up to the 561-580 mm whiting length interval. Thereafter, the curve

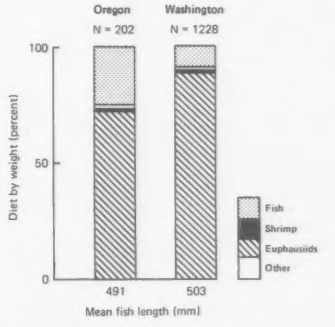

FIGURE 2.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, taken off Oregon and Washington, summer 1967.

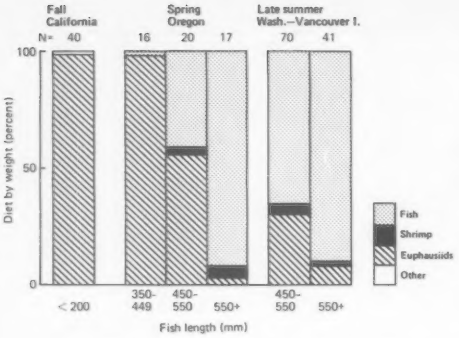

FIGURE 3.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, for different length groups of whiting at various locations in 1980.

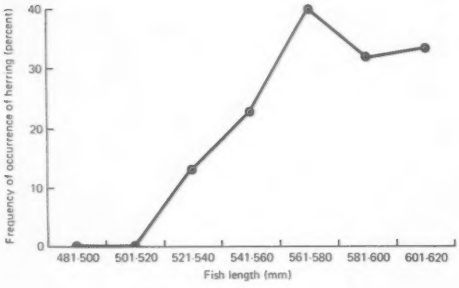

FIGURE 4.—Percent frequency of occurrence of Pacific herring, *Clupea harengus pallasi*, in stomachs of different length groups of Pacific whiting, *Merluccius productus*, taken late summer 1980 off Washington and Vancouver Island.

appears to level off at a 30% occurrence of Pacific herring.

The difference in Pacific whiting diets between the years 1967 and 1980 is mainly seen as a greater percent consumption of fish in 1980 by whiting >450 mm. No clear explanation is available because sample size in 1980 was small and samples were obtained further offshore than in 1967. The most distinct relationship noted in these results is the tendency of Pacific whiting to consume prey species which occur in patches or schools, usually euphausiids and pelagic fishes such as eulachon, northern anchovy, and Pacific herring which also prey on euphausiids (Wailes 1936; Barraclough 1964; Barraclough et al. 1968). Likewise, the majority of the invertebrate prey of Pacific whiting (e.g., pandalid, sergestid, and pasiphaeid shrimp) are documented predators of euphausiids (Renfro and Pearcy 1966; Pearcy 1970; Judkins and Fleminger 1972). Thus, euphausiids appear to be the unifying factor, their presence attracting not only the Pacific whiting but also other organisms which then become available prey for Pacific whiting.

Alton and Nelson (1970) reported the main food items of Pacific whiting off northern Oregon and Washington to be euphausiids, eulachon, and pandalid shrimp. Similarly, Outram and Haegele (1972) found euphausiids, pandalid shrimp, and schooling fish (such as Pacific sand lance, *Ammodytes hexapterus*; Pacific herring; and eulachon) most frequently in stomachs of Pacific whiting sampled off Vancouver Island. They also found Pacific herring to be a more important component in the diet of large Pacific whiting. Off California, Gotshall (1969a) discovered pandalid shrimp, euphausiids, flatfish, and schooling fish constituted most of the whiting's food. Although Gotshall (1969a, b) showed that on the average pandalid shrimp dominated the Pacific whiting diet, in some months fish or euphausiids were found to be the primary food items. This seasonal change in diet may have resulted from the changing size composition of the Pacific whiting population in the study area due to northward migration of adults in spring.

Predator-Prey Size Relationship

An examination of the relationship between a fish predator's size and its choice of prey sizes may aid in understanding, interpreting, and quantifying a predator's feeding habits (Ursin 1973; Werner 1974; Agger and Ursin 1976; Werner and Hall 1977; Hahm and Langton 1980). Calculation of the frequency distribution of predator weight to prey weight ratios, as described by Ursin (1973), quantifies a predator's food size preference through central tendency measures of its distribution. These measures can then be used directly as input parameters to models such as Andersen and Ursin's (1977) multispecies Beverton and Holt model or the various multispecies VPA models (Helgason and Gislason 1979; Sparre 1980).

The basic method of calculating predator-prey size ratios utilizes the total weight in grams (W_j) and total number (ΣN_j) of each prey type j in a collection of predator stomachs. The individual mean weight of each prey type ($\bar{w}_j$) is calculated and compared with the mean predator weight ($\bar{w}_j$). Ursin (1973) discovered that for benthic-feeding fish the frequency distribution of the ratios of predator weight to prey weight ($\bar{w}_j/\bar{w}_j$) was approximately log-normal in shape. Therefore, a plot of ln ($\bar{w}_j/\bar{w}_j$) vs. ΣN_j should be a normally shaped curve.

This methodology was applied to the 1980 Pacific whiting stomach data. There was a total of 204 Pacific whiting in this sample, ranging in length from 116 to 645 mm, with $\bar{w}_i$ of 862 g. These Pacific whiting consumed a total of 8,940 food items [$\Sigma(\Sigma N_j)$] with individual $\bar{w}_j$ ranging from 0.002 g for amphipods to 83 g for a medusafish, *Icicthys lockingtoni*.

The solid lines in Figures 5-7 represent the shape of the predator-prey size curves resulting from the analysis of 1980 data when separated into three predator size groups. However, these curves do not necessarily represent the prey-size preference of Pacific whiting. Lawlor (1980) stated that the proportion of a food item in the diet of a predator is a function not only of the predator's choice for that item but also of the item's availability. Only when abundances of all prey items are equal, do the observed proportions of prey items in a predator's stomach reflect the predator preference.

To determine the prey-size preference of Pacific whiting, we may examine a theoretical situation in which equal numbers of each prey size are offered to the Pacific whiting. Assuming the numbers of each prey type in the environment to be inversely proportional to the prey type's weight (Ursin 1973), this situation can be created by multiplying total ΣN_j by $\bar{w}_j$. To adjust for predator size, this quantity is divided by $\bar{w}_i$. The dashed lines in Figures 5-7 depict the theoretical results of offering equal numbers of each prey size to the whiting.

Pacific whiting <200 mm, whose diet consisted mainly of euphausiids, have a very narrow prey-size selection curve (Fig. 5) which reflects their choice of a narrow size range of food. The dashed line of the pre-

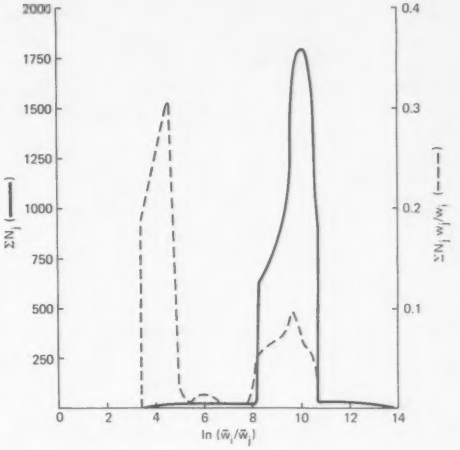

FIGURE 6.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators 350-549 mm long with an average weight ($\bar{w}_i$) of 876.2 g, under natural (—) and simulated (---) conditions.

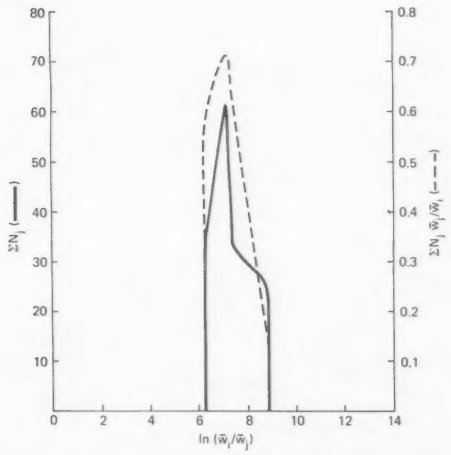

FIGURE 5.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators <200 mm long with an average weight ($\bar{w}_i$) of 13.2 g, under natural (—) and simulated (---) conditions.

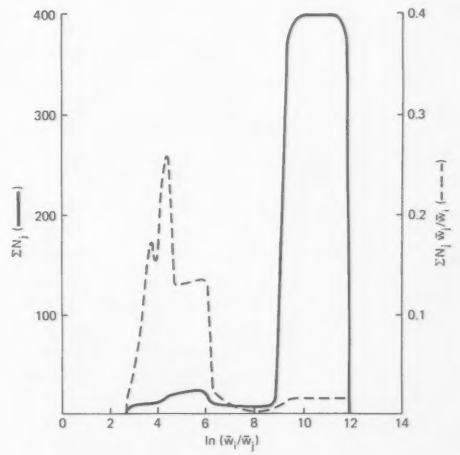

FIGURE 7.—Frequency distribution of predator-prey size scores for Pacific whiting, *Merluccius productus*, predators 550+ mm long with an average weight ($\bar{w}_i$) of 1,441.3 g, under natural (—) and simulated (---) conditions.

ference curve for the small Pacific whiting closely follows the selection curve in which euphausiid-sized prey dominated.

The selection curve for the middle-sized group of Pacific whiting, 350-549 mm, also peaks sharply but with long, trailing ends indicating that euphausiids dominated the diet in numbers although small numbers of prey items, both smaller and larger than euphausiids, were eaten (Fig. 6). The preference curve is bimodal with the largest mode corresponding to a predator-prey size ratio of about 100:1, while the second mode reflects a continuing preference for euphausiid-sized items.

The largest size group of Pacific whiting, 550+ mm, have an actual prey-size curve which depicts the numerical dominance of euphausiids in their food by the sharp peak at ln $(\bar{w}_i/\bar{w}_j)$ value of about 10.5 (Fig. 7). There is also a pronounced hump in the left tail of the curve in the region of a predator-prey weight ratio corresponding to a large Pacific whiting predator and a Pacific herring-sized prey. The preference curve shifts completely away from the selection curve for these Pacific whiting. The mode for euphausiid prey is dampened almost completely and the most prevalent predator-prey size ratio is about 130:1, equivalent to the ratio of a large Pacific whiting predator to a Pacific herring-sized prey.

Thus, it appears that the diets of Pacific whiting <200 mm long reflect a preference for euphausiid-sized prey. Although the 350-549 mm size group of Pacific whiting shows a dominant prey-size preference of 100:1, the calculated preference curve deviates from the predicted normal shape due to a second mode in the region corresponding to euphausiid-sized prey. Deviations from normality can be caused when the abundance of a naturally occurring prey item is not inversely proportional to its weight as assumed or when the prey occur in such dense patches that the predator consumes more than one prey item at a time (Ursin 1973). The latter case is a likely description of Pacific whiting predation on euphausiids, though this would have to be verified through direct observation. The largest size group of Pacific whiting shows a preference for Pacific herring-sized prey with a median predator-prey size ratio of about 130:1. This is similar to Ursin's (1973) calculation of an average predator-prey size ratio of 160:1 for Atlantic cod, *Gadus morhua*.

The prey-size preference of Pacific whiting is reasonably described by Ursin's model. The major parameters which define the shape of the prey-size preference curve are the mean ($\bar{x}$) and variance (s^2) of the frequency distribution of predator-prey size scores (Table 3) when equal numbers of prey sizes are offered to the predator. These parameters are $\bar{x} = 7.16$, $s^2 = 0.42$ for <200 mm fish; $\bar{x} = 6.48$, $s^2 = 7.18$ for 350-549 mm fish; and $\bar{x} = 4.88$, $s^2 = 2.40$ for 550 + mm fish.

Diel Feeding Pattern

A total of 258 Pacific whiting stomachs (7 of which were empty) were taken at 7 different times of day during a 15-h period at a location off the Washington coast in July 1967. To detect any discontinuity in feeding during this period, a one-way analysis of covariance was performed using the model

$$y = \mu + a_i + bx_i,$$

where y is the weight of the stomach contents and x is the Pacific whiting weight. If the stomachs are grouped by time, i, then the test of among-time variation in the weight of stomach contents after adjustment for Pacific whiting weight is the test of the equality of the intercepts, a_i, given a common slope, b (Jenkins and Green 1977). The F-ratio for this test is the among-group variance estimate divided by the within-group variance estimate.

Figure 8 plots mean stomach content weight as a percentage of Pacific whiting weight for samples taken during the 15-h period in July 1967. Stomach content weight per fish weight is highest at 1800 h, with a value of 2.5%, and slightly increases between 0100 and 0300 h and between 0400 and 0900 h. Despite the great variability among all time periods, the analysis of covariance of the data rejects the null hypothesis of no difference between group means of stomach content weight at the 0.01 level of significance [$F(6,243\ \text{df}) = 7.83$]. Therefore, feeding by Pacific whiting was discontinuous during the sampling period.

Stomach fullness was highest in early evening (1800 P.S.T.), with some increases after midnight (0300 P.S.T.) and morning (0900 P.S.T.). These fullness peaks coincide with the times of euphausiid, *Thysanoessa spinifera*, concentration in the same portion of the water column where the Pacific whiting are concentrated—nearbottom at evening and morning and nearsurface after midnight (Alverson and Larkins 1969; Alton and Blackburn 1972).

Hickling (1927) noted that stomachs of European hake, *Merluccius merluccius*, were fullest at midnight. He also suggested that European hake migrate vertically in search of euphausiids. Silver hake, *Merluccius bilinearis*, of the northwest Atlantic also feed nocturnally, starting their feeding activity after dusk and actively feeding until midnight (Bowman and Bowman 1980). Thus, fish of the genus *Merluccius*

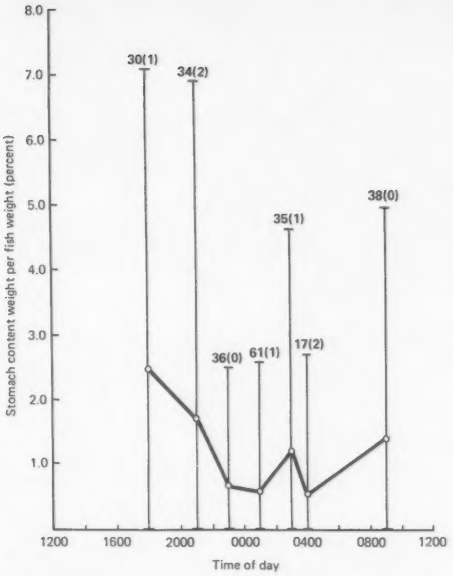

FIGURE 8.—Mean stomach content weight as a percentage of Pacific whiting, *Merluccius productus*, weight over part of a 24-h period at a diel sampling location off the Washington coast in July 1967 (vertical bars indicate the range of values in a given time period). Numbers of stomachs containing food are noted above each time period, with numbers of empty stomachs in parentheses.

have similar nocturnal feeding habits, although the timing of peaks in stomach fullness is not identical.

Daily Ration

An estimate of the average food intake by a fish predator is needed to evaluate predation mortality rates of prey species in some models (Majkowski and Waiwood 1981). Daily ration is a useful measure of food intake and can be calculated from field data if there exists an estimate of the gastric evacuation rate (Eggers 1977; Elliott and Persson 1978). The total 1967 Pacific whiting data set, containing 1,749 stomach samples, is used here to compute daily ration, since it includes a large number of samples taken at many different times of day and records of the number of empty stomachs present in the samples which is necessary for daily ration calculation.

The Elliott and Persson (1978) model which assumes an exponential, temperature-dependent evacuation rate, R, is applied to the data set for the daily ration computations. If stomach samples are collected at intervals of t hours, the mean stomach content weight as a percentage of fish weight, S_i, in each interval i is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978) the daily ration in terms of percentage body weight, ΣC_t, can then be evaluated by the following expression:

$$\Sigma C_t = \frac{Rt}{1 - e^{-Rt}} \sum_{i=1}^{m} S_i (1 - e^{-Rt}) = 24\bar{S}R \quad (1)$$

where $\bar{S} = \Sigma S_i/\mathrm{m}$. Durbin and Durbin (1980) found that the relationship between R and water temperature T for marine fish eating small food organisms was

$$R = 0.416e^{0.105T}. \quad (2)$$

This Equation (2) was used to calculate R here, since most prey eaten by Pacific whiting in 1967 were small organisms, mainly euphausiids. Some error is introduced at this point because part of the diet consisted of fish which are evacuated at a slower rate than small crustaceans (Durbin et al. 1980). Water temperature was assumed to be 8.2°C, the approximate monthly mean temperature for July at 60 m below surface in the Washington-Oregon coastal region (Robinson 1976) where most of the fish were collected.

The calculated daily ration of Pacific whiting, using Equations (1) and (2) on the 1967 data, is equal to 2.5% body weight/d for an average Pacific whiting size of 500 mm. Although this estimate is probably high, due to the use of the evacuation rate only for small crustaceans, it is comparable to other estimates. Daily ration estimates for a similar fish—adult silver hake in the northwest Atlantic—range between 0.6 and 2.7% body weight/d (Durbin et al. 1980; Cohen and Grosslein 1981; Pennington 1981). The present estimate is reasonable but should be verified further before it is used in calculating energy budgets for Pacific whiting.

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FOOD OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN AN EMBAYMENT OF SOUTHEASTERN ALASKA

The walleye pollock, *Theragra chalcogramma* Pallas, is commercially and ecologically one of the most important fishes in Alaskan waters. In recent years, it has predominated by weight in the catches of commercial groundfish and in demersal trawling surveys of the Bering Sea and the Gulf of Alaska (North Pacific Fishery Management Council 1979a, b; Pereyra et al. 1976[1]; Ronholt et al. 1978[2]). It is similarly abundant in the inside waters of southeastern Alaska (Carlson et al. 1977[3]), where recent attempts have been made to establish a commercial fishery for walleye pollock. Walleye pollock are also an important component of the food web, primarily as forage for seabirds, marine mammals, and fish. In the eastern Bering Sea, walleye pollock is the most important species in the diet of many seabirds (Hunt et al. 1981) and is a major food of seals, *Phoca* spp. (Lowry and Frost 1981); whales (Frost and Lowry 1981); and northern fur seals, *Callorhinus ursinus* (Harry and Hartley 1981). In southeastern Alaska, juvenile walleye pollock are one of the most common foods of troll-caught Pacific salmon, *Oncorhynchus* spp. (Wing 1977).

Despite the importance of walleye pollock, their diet has been little studied. The food of adults and juveniles from the eastern Bering Sea has been investigated during the spring, summer, or fall (Takahashi and Yamaguchi 1972; Mito 1974; Bailey and Dunn 1979), but no single study covered more than one season in a given area. There are no published data on the food of walleye pollock in the eastern North Pacific Ocean south of the Bering Sea except for one report of their feeding upon salmon fry in southeastern Alaska (Armstrong and Winslow 1968). In this report, I document the foods and seasonal changes in the diet of walleye pollock for 1 yr in an area of the inside waters of southeastern Alaska.

Methods

During each of the four seasons, stomachs were collected from walleye pollock in two adjacent bays, Auke Bay and Fritz Cove, near Juneau, Alaska (Table 1; Fig. 1). The two bays make up a larger embayment of Stephens Passage, a prominent fjord in the inside waters of southeastern Alaska. Depending upon the availability of research vessels, fish were caught with three types of bottom trawls: A 400-mesh (27 m) Eastern otter trawl, a standard 40-ft (12 m) Gulf shrimp trawl, and a 12-ft (3.7 m) balloon-type otter trawl. All trawling was done during daylight. The trawls were dragged from deeper to shallower water during each haul, so the exact depth at which fish were captured could not be determined. Trawling depths averaged 46 m (range 16-60 m) in Auke Bay and 90 m (range 55-110 m) in Fritz Cove. It was necessary to collect walleye pollock from both bays to obtain a broad size range of fish in each season. When a single tow produced large numbers of walleye pollock, the catch was arbitrarily sampled to obtain about 40 fish in each 100 mm size category; otherwise, all walleye pollock were retained. Standard length (SL) of each retained fish was measured, sex determined when possible, and stomachs removed and preserved in 5% buffered Formalin[4]. Walleye pollock used for the stomach samples were mostly between 150 and 450 mm SL, and ranged from 106 to 585 mm SL. Most of these fish were probably juveniles or young adults because walleye pollock mature at lengths between 290 and 350 mm FL (fork length) (Hughes and Hirschhorn 1979).

A number of authors have discussed various techniques for analyzing stomach contents of fish (see Windell 1971), and it appears that any single method

[1]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Processed rep., 619 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[2]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948-1976, a historical review. Processed rep., 4 vols., 955 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[3]Carlson, H. R., R. E. Haight, and K. J. Krieger. 1977. Species composition and relative abundance of demersal marine life in waters of southeastern Alaska, 1969-77. Processed rep., 69 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, 2725 Montlake Boulevard E., Seattle, WA 98112.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of walleye pollock stomach samples collected each season, by date and location of collection, Auke Bay and Fritz Cove, southeastern Alaska, 1979-80.

Season	Dates of collection	Number of trawl hauls	Number of stomachs collected		
			Auke Bay	Fritz Cove	Total
Summer	July, August 1979	11	105	62	167
Fall	October, November 1979	6	64	113	177
Winter	January 1980	4	81	67	148
Spring	April 1980	2	39	46	85
Totals			289	288	577

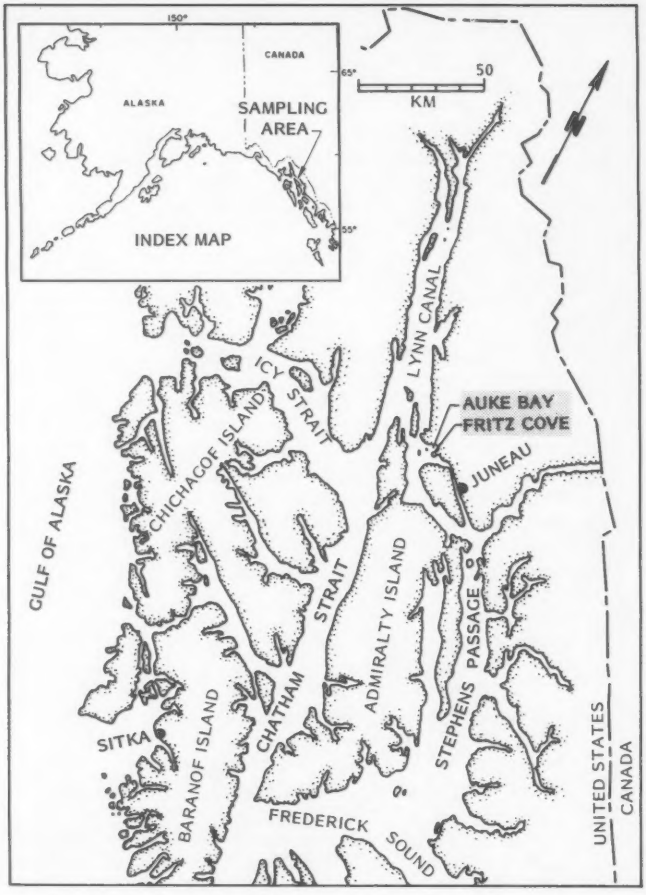

FIGURE 1.—Location of Auke Bay and Fritz Cove, southeastern Alaska, where stomachs were collected from walleye pollock in 1979-80.

has its biases. Therefore, I chose to analyze the stomach contents of walleye pollock in two ways: 1) Percent by volume of major food categories to show the contribution in biomass of the foods, and 2) percent frequency of occurrence to show the diversity of foods at lower taxonomic levels.

To determine percent by volume, I either measured or estimated the volume of major food categories (e.g., mysids, shrimp, or fish) in each stomach, depending upon the amount of food present. In walleye pollock with stomach contents about ≥ 0.5 ml, the displacement volume of food in each major category was measured in a graduated cylinder and then expressed as a percentage of the total volume of the stomach contents. In fish with stomach contents <0.5 ml, food was divided by categories into piles of uniform height in a petri dish and placed over a grid. The number of grid squares covered by each pile was used to estimate the volume percentage of each food category. I then pooled percent-volume measurements and estimates for all fish and calculated mean percentages for each food category. Walleye pollock with empty stomachs or with stomachs containing only a trace of food were excluded from these calculations. Many stomachs contained a large percentage of flocculent, digested matter or an indistinguishable mixture of crustacean parts; these items were termed "unidentified digested matter" and "unidentified crustacean fragments," respectively.

To determine the frequency of occurrence of foods, each item present in a stomach was identified to the lowest practical taxon. Percent frequency of oc-

currence for the food item was calculated by dividing the number of stomachs that contained the item by the total number of walleye pollock stomachs. Stomachs with a trace of food were included in this analysis, but empty stomachs were not.

The volumetric data were categorized by size and sex of walleye pollock and by season of year (for dates, see Table 1) to determine if these factors influenced the diet. To compare types of food eaten by different sizes of walleye pollock, the fish were arbitrarily divided into three length groups: Small, <250 mm; intermediate, 250-349 mm; and large, >349 mm SL. The percent of empty stomachs was also calculated for each season and size category as an indicator of seasonal feeding activity. Because the size of walleye pollock was generally different in each bay during the same season, the foods of the fish in the two bays could not be compared. Consequently, data for the two bays were pooled for all analyses. Differences in feeding at different depths also could not be analyzed because, as previously noted, the precise depth where fish were caught was unknown.

Results and Discussion

When data from all samples of walleye pollock were combined (regardless of size, sex, or season), crustaceans were the major food. Of the crustaceans, euphausiids and mysids had the highest percent volumes and frequencies of occurrence (Tables 2, 3). *Thysanoessa raschii* was the most frequently eaten euphausiid; *Acanthomysis pseudomacropsis* and *Neomysis kadiakensis* were the most frequently eaten mysids. The percent volume of shrimp was nearly as high as the percent volume of euphausiids and mysids; however, shrimp were eaten less frequently. Most of the shrimp were either *Crangon* spp. (Crangonidae) or Pandalidae. Copepods, hyperiid and gammarid amphipods, and cumaceans were found in many of the stomachs (>20%), but their percent volumes were small (<3%). Often stomachs contained only one or two individuals that comprised a minute fraction of the contents. Copepods were mostly *Metridia* sp. and *Calanus* sp.; cumaceans were mostly *Eudorella* sp. Amphipods were generally not identified to species.

Fish and, to a lesser degree, polychaetes were the only other foods present in amounts greater than a trace. They were found less frequently than crustaceans and were usually identifiable only to class. However, compared with crustaceans, fish found in the stomachs were relatively large and usually composed most of the volume of food in the stomachs, when they occurred.

The common food organisms in all of the studies of walleye pollock have been crustaceans and fish. In the eastern Bering Sea in summer 1970, walleye pollock fed almost exclusively on euphausiids, copepods, and fish (Takahashi and Yamaguchi 1972). In fall 1972, walleye pollock there ate euphausiids and fish (Mito 1974); and in summer 1974 and spring 1977, they ate mostly euphausiids, copepods, fish, and amphipods (Bailey and Dunn 1979). In southeastern Alaska in 1979-80 (my study),

TABLE 2.—Mean percent volume of major categories of food in walleye pollock stomachs from Auke Bay and Fritz Cove, southeastern Alaska, 1979-80. (Table does not include empty stomachs or those with only a trace of food.)

Food category	All fish (%)	By length (SL) category of fish			By sex of fish[1]	
		<250 mm (%)	250-349 mm (%)	>349 mm (%)	Males (%)	Females (%)
Euphausiids	17.1	16.6	21.4	8.5	19.3	18.8
Mysids	14.8	21.4	9.9	6.5	11.7	10.2
Shrimp:	14.3	7.7	13.8	35.6	15.5	18.3
Pandalids	7.3	1.7	7.1	25.2	8.7	9.6
Crangonids	5.3	4.7	5.0	7.6	4.0	7.0
Hippolytids	0.6	0.9	0.5	0.1	0.2	1.3
Unidentified shrimp	1.1	0.4	1.2	2.7	2.6	0.4
Fish	5.7	3.7	4.6	14.7	5.7	6.7
Cumaceans	2.8	3.8	2.4	0.8	2.2	1.5
Polychaetes	2.4	0.7	4.5	2.5	3.0	3.1
Copepods	2.2	4.0	0.6	0.5	0.3	1.4
Gammarid amphipods	1.6	1.9	1.3	1.4	1.9	1.3
Hyperiid amphipods	1.2	1.2	1.3	0.9	1.8	0.8
Unidentified crustacean fragments	9.7	10.6	8.8	9.3	9.0	7.2
Other foods	2.0	2.0	0.9	4.5	1.0	2.6
Unidentified digested matter	26.2	26.4	30.5	14.8	28.6	28.2
Mean length of pollock (mm)	261.3	193.9	292.0	394.9	283.8	283.2
Number of samples	431	204	161	66	150	190

[1]91 additional fish were examined for which sex could not be determined.

TABLE 3.—Frequency of occurrence of food items found in at least 1% of stomachs of 541 walleye pollock from Auke Bay and Fritz Cove, southeastern Alaska, 1979-80[1]. (Table does not include an additional 36 stomachs that were empty.)

Food item	Frequency of occurrence (%)
Mysids	54
Acanthomysis pseudomacropsis	19
Acanthomysis nephrophthalma	5
Neomysis kadiakensis	18
Neomysis rayii	3
Neomysis sp.	1
Pseudomma truncatum	7
Unidentified mysids	9
Euphausiids	47
Thysanoessa raschii	31
Thysanoessa spinifera	1
Thysanoessa longipes	1
Unidentified euphausiids	17
Copepods	42
Metridia sp.	20
Calanus sp.	15
Euchaeta elongata	6
Aetidius sp.	6
Centropages abdominalis	2
Unidentified copepods	6
Hyperiid amphipods	29
Parathemisto sp.	6
Unidentified hyperiids	23
Shrimp	28
Pandalid shrimp	11
Pandalus borealis	3
Pandalus tridens	1
Unidentified pandalids	9
Crangonid shrimp	14
Crangon communis	2
Crangon dalli	2
Crangon franciscorum	1
Crangon sp.	6
Unidentified crangonids	4
Hippolytid shrimp	4
Eualus avinus	1
Unidentified hippolytids	3
Unidentified shrimp	5
Gammarid amphipods	35
Oetocerotidae	4
Cyphocaris challengeri	1
Unidentified gammarids	21
Cumaceans	21
Eudorella sp.	16
Leucon sp.	2
Unidentified cumaceans	3
Polychaetes (unidentified)	12
Fish	10
Theragra chalcogramma	1
Unidentified fish	8
Cephalopods	1
Pelecypods	1
Isopods	1
Larval shrimp	1
Larval brachyuran crab	1
Larval anomuran crab	1

[1]Also present at frequencies <1%: Mysids—*Pseudomma berkeleyi, Meterythrops* sp., *Holmesiella anomula, Stilomysis grandis*; pandalid shrimp—*Pandalopsis dispar*; crangonid shrimp—*Crangon alaskensis, Argis crassa*; fish—*Clupea harengus pallasi*, Osmeridae, Pleuronectidae, Stichaeidae; cumaceans—*Cumella* sp.; copepods—*Calanus cristatus, Pseudocalanus* sp.; hyperiid amphipod—*Primno macropa*; cephalopod—*Octopus* sp.; unidentified gastropods; Paguridae—*Pagurus ochotensis*; brachyuran crab; barnacle cyprid; larval fish—*Thaleichthys pacificus*; Holothuroidea—*Molpadia intermedia*; algae.

walleye pollock consumed primarily euphausiids, mysids, shrimp, and fish. Thus, of the crustaceans, euphausiids were a major food in all studies, whereas the types of other crustaceans varied among the investigations. Shrimp, an important food for walleye pollock both in my study and near Kodiak Island[5], were found only in very small amounts in Bering Sea fish. In all studies, organisms that are strictly benthic (e.g., clams and crabs) were conspicuously scarce in the diet.

In fishes, the size of prey generally increases as the size of predators increases (Nikolsky 1963), and this appears to be true in walleye pollock. In my study, small walleye pollock ate mostly planktonic crustaceans, particularly euphausiids, mysids, and copepods; large walleye pollock generally ate larger prey, such as shrimp and fish (Table 2). Intermediate-sized walleye pollock were transitional in their diet and ate a combination of large and small foods. In the Bering Sea, juvenile walleye pollock (<350 mm) also ate mostly euphausiids or copepods, whereas larger walleye pollock ate larger foods, primarily fish (Takahashi and Yamaguchi 1972; Mito 1974; Bailey and Dunn 1979). Walleye pollock became increasingly cannibalistic with increase in size in the Bering Sea: More than half the food of fish >550 mm FL was smaller walleye pollock (Takahashi and Yamaguchi 1972). In my study, cannibalism was observed in only 1% of the stomachs (Table 3); however, few walleye pollock >450 mm SL were examined.

Sex of the fish had little effect on their diet (Table 2). The diets of male and female walleye pollock were nearly identical in percent volume of each food category.

Walleye pollock apparently fed year-round (Table 4): In any one season only 4-8% of all fish had empty stomachs. In any one size group, no more than 14% of the fish had empty stomachs in any season. In con-

[5]P. Livingston, Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, unpubl. data.

TABLE 4.—Seasonal feeding activity of walleye pollock shown by percent of fish with empty stomachs, Auke Bay and Fritz Cove, southeastern Alaska, 1979-80.

Size	Stomachs examined	Spring	Summer	Fall	Winter
All sizes	Total (no.)	85	167	177	148
	With food (no.)	82	158	162	139
	Empty (%)	4	5	8	6
<250 mm SL	Total (no.)	14	91	99	83
	With food (no.)	14	84	92	76
	Empty (%)	0	8	7	8
250-349 mm SL	Total (no.)	51	36	57	53
	With food (no.)	48	35	52	51
	Empty (%)	6	3	9	4
>349 mm SL	Total (no.)	20	40	21	12
	With food (no.)	20	39	18	12
	Empty (%)	0	3	14	0

trast, in a seasonal 1-yr study of food of adult walleye pollock off Hokkaido Island, Japan, the rate was much higher, particularly during the winter months when up to 80% of the stomachs were empty (Maeda et al. 1981). In an eastern Bering Sea study (Bailey and Dunn 1979), generally few walleye pollock had empty stomachs in summer 1974 (results similar to those of my study); however, a much higher percentage of fish had empty stomachs there in spring 1977 than in my study.

The diet of small walleye pollock varied widely from season to season in the percent volume of each food type (Fig. 2). Euphausiids were the predominant food of small walleye pollock in winter and spring (34% and 78%, by volume, respectively) but constituted <7% of the stomach contents in the summer and fall. Conversely, mysids were the predominant food in the summer and fall diets (36% and 22%, by volume, respectively) but were much less important in the winter and spring (<5%, by volume). Copepods were also an important food (11%, by volume) in the summer but were insignificant (<1%) in other seasons.

For each season, the diet of intermediate-sized

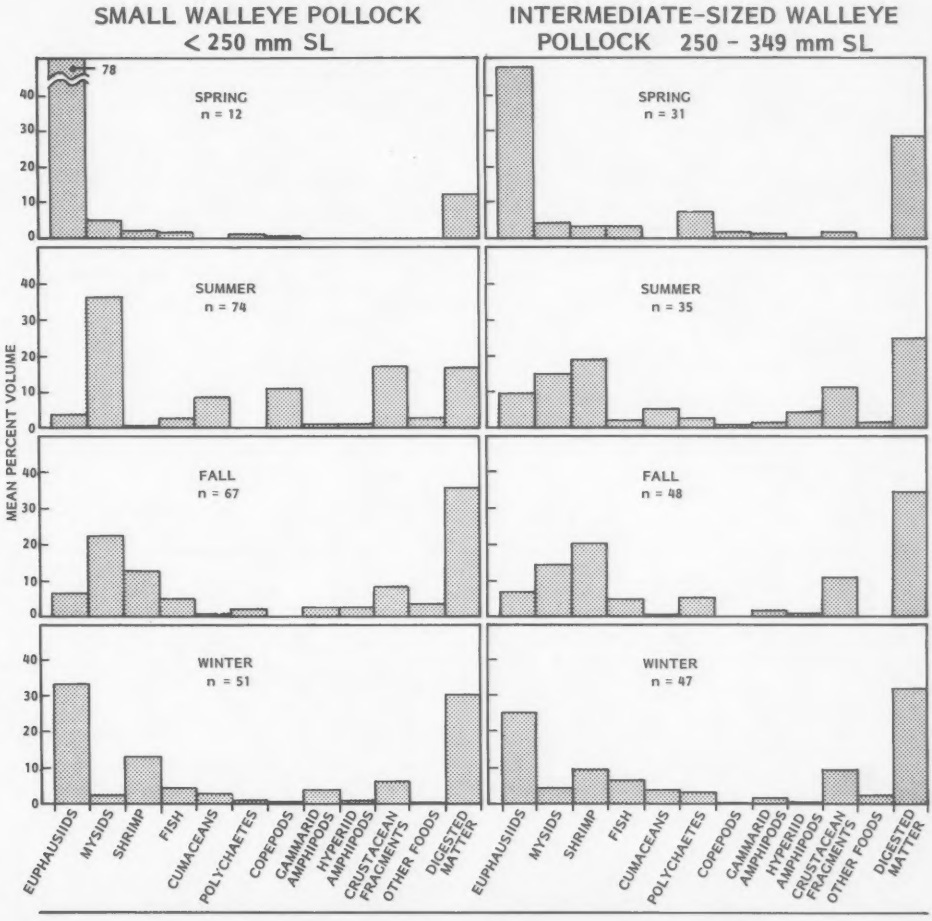

FIGURE 2.—Mean percent volume of major food categories in stomachs of small and intermediate-sized walleye pollock by season of year, Auke Bay and Fritz Cove, southeastern Alaska, 1979-80. (Figures do not include empty stomachs or those with only a trace of food.)

walleye pollock was similar to that of small walleye pollock (Fig. 2). Intermediate-sized fish also fed predominately on euphausiids in the winter and spring and more on mysids in the summer and fall. However, seasonal variability in diet was not as great as for small walleye pollock. Too few large walleye pollock were collected in three of the seasons to demonstrate seasonal changes in their foods.

Some of the seasonal differences found in foods of small walleye pollock may be explained by the availability of euphausiids and copepods. In two seasonal studies of zooplankton in the Auke Bay vicinity, 1962-64 (Wing and Reid 1972) and 1973-75 (Carlson 1980), euphausiids (excluding small larval forms) were least abundant and copepods were most abundant during the late spring and summer. Similar seasonal patterns were found in the foods of small walleye pollock: The percent volume of euphausiids was lowest in the summer, whereas copepods were a significant food only during the summer. However, results of the zooplankton studies also differ in some respects from my results: In 1973-75, euphausiids were most abundant in plankton in the fall (Carlson 1980), but in my 1979-80 study, they were relatively scarce in the stomach samples during the fall. Concurrent studies of walleye pollock foods and zooplankton abundance are needed to better understand the causes of seasonal variations in the diet of small walleye pollock.

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SUMMER FOODS OF TEXAS COASTAL FISHES RELATIVE TO AGE AND HABITAT

Age and habitat are often ignored as factors which simultaneously influence the diets of demersal fishes. Studies of fish foods by age (size) or habitat (depth of capture, substrate) either summarize foods over all sizes and depths (Henwood et al. 1978), construct several size or depth groupings to equalize sampling effort (Overstreet and Heard 1978; Mericas 1981), or establish arbitrary size or capture depth ranges for ontogenetic or depth-related analyses (Rogers 1977; Divita et al. 1983). In this paper, we analyze the stomach contents of seven species of Texas coastal fishes with respect to both age and habitat.

Materials and Methods

Fishes examined in our study were taken from trawl catches by the NOAA RV *Oregon II* and the Texas Parks and Wildlife Department RV *Western Gulf* between sunset and sunrise in waters 7-73 m deep along the entire Texas coast. Each vessel towed a 12.2 m semiballoon trawl with tickler chain at 5-6 km/h. The species collected from the family Sciaenidae are sand seatrout, *Cynoscion arenarius*; silver seatrout, *C. nothus*; spot, *Leiostomus xanthurus*; and Atlantic croaker, *Micropogonias undulatus*; from the family Sparidae, longspine porgy, *Stenotomus caprinus*; and from the family Trichiuridae, Atlantic cutlassfish, *Trichiurus lepturus*. Fishes were collected by depth ranges (7-17, 18-44, or 45-73 m) and preserved in 3.7% formaldehyde-seawater. These depth ranges correspond to distinctive habitats (substrates) as reported by Grady (1971), Flint and Rabalais (1980), and Gallaway and Reitsema (1981): sand or muddy-sand (7-17 m), sand-silt-clay (18-44 m), and silty-sand or silty-clay (45-73 m).

In the laboratory, fishes from each depth range were measured (standard length, SL, or total length, TL, where applicable) and further separated into either age-0 or age-I classes, based upon data summarized by the Gulf of Mexico Fishery Management Council (1980) or upon unpublished personal data on gonadal maturation. Fishes were presumed to have reached age I at the following lengths: longspine porgy, 75 mm SL; spot, 100 mm SL; Atlantic croaker, 125 mm SL; sand and silver seatrouts, 150 mm SL; hardhead catfish, 200 mm SL; and Atlantic cutlassfish, 400 mm TL. No age II individuals were collected. For each species, the stomach contents of all individuals in a given age/depth category were combined and washed through sieves to separate similar-sized food items (Carr and Adams 1972), which were identified and enumerated microscopically and then dried at 80°-90°C for 24 h. The dry weights of the various food items were calculated from their numerical proportions and converted to percentages of total food dry weight. Stomach contents were identified to broad but exclusive categories such as sand, diatoms, shrimps, or fishes. Fish bones and scales without associated flesh were often found in hardhead catfish stomachs and were thus given a category. Animal fragments not distinctly referable to any taxon were also categorized. Fine organic matter not referable to any other category was termed detritus. Prey fishes, shrimps, and crabs were identified to family or genus when possible. Within each species, diet similarities among age/depth categories were compared by the Spearman rank correlation coefficient, r_s (Fritz 1974).

Results

The stomach contents of the four sciaenid fishes are summarized in Table 1, and those of the other three species in Table 2. Intraspecific diet similarities are given in Table 3. The effect of depth of capture on diets of spot and Atlantic cutlassfish could not be evaluated, since the majority of individuals were collected from a single depth range (7-17 m and 18-44 m, respectively). Correlations between diets of age-0 and age-I spot ($r_s = 0.069$) and between diets of age-0 and age-I Atlantic cutlassfish ($r_s = 0.399$) were not significant. Age-0 spot consumed more infaunal organisms, such as polychaetes and nematodes, and nearly twice as much detritus as age-I spot, which captured proportionately more epifaunal prey such as fishes, amphipods, and shrimps. While both age classes of Atlantic cutlassfish preyed primarily upon fish, age-I individuals also exploited squids. Small sample size (three stomachs) for the age-0 Atlantic cutlassfish is probably responsible for the lack of diet correlation.

Sand and silver seatrouts fed both in the water column and near the bottom. Diets of three of the four age/depth categories of sand seatrout were significantly correlated, primarily because fishes and shrimps were the favored prey. The exception was the diet of age-0 sand seatrout in 18-44 m waters in which squids were the primary prey. The most frequently identified sand seatrout prey taxa were anchovies, *Anchoa*, and roughback shrimp, *Trachypenaeus* sp. Silver seatrout also preyed upon fishes and shrimps, but only the age-0 diets in the two inhabited depth ranges were correlated. The data on

TABLE 1.—Stomach contents of sand seatrout, silver seatrout, spot, and Atlantic croaker collected from Texas coastal waters between 4 June and 3 July 1981, expressed as percentages of total food dry weight by age and depth of capture. A "+" indicates presence in the diet but <0.1%. Fish lengths are mm SL, depth ranges in meters.

Stomach contents	Age:	Sand seatrout				Silver seatrout				Spot		Atlantic croaker			
		0		I		0		I		0	I	0		I	
	Depth:	7-17	18-44	7-17	18-44	7-17	18-44	7-17	18-44	7-44	7-44	7-17	18-44	7-17	18-44
Diatoms		—	—	—	—	—	—	—	—	0.6	0.9	—	—	—	—
Nematodes		+	—	—	—	—	—	—	—	3.8	0.4	0.1	—	—	—
Polychaetes		0.4	—	—	—	0.1	—	—	—	7.3	3.9	61.2	35.9	4.3	38.1
Bivalves		—	—	—	—	—	—	—	—	1.8	1.2	—	—	—	—
Squids		—	47.5	—	—	—	—	—	19.7	—	—	0.2	—	—	—
Copepods		+	—	—	—	—	—	—	—	5.2	0.6	+	+	+	—
Stomatopods		+	—	+	—	0.3	0.2	—	11.4	—	—	—	—	—	—
Mysids		0.5	—	+	—	3.0	0.1	0.6	—	1.4	—	0.7	—	—	0.6
Cumaceans		—	—	—	—	0.1	—	—	—	0.8	2.0	—	—	—	—
Isopods		—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
Amphipods		0.2	—	—	—	+	—	0.3	—	2.2	4.3	0.2	—	—	—
Crabs		0.9	—	7.2	4.4	4.3	—	1.2	+	—	—	5.9	0.3	76.5	—
Shrimps		2.0	24.7	59.5	40.3	6.7	16.8	88.9	12.9	4.8	6.6	8.6	35.6	9.0	16.3
Holothurians		—	—	—	—	—	—	—	—	—	—	—	9.4	6.7	—
Tunicates		—	—	—	—	—	—	—	—	—	—	—	—	—	30.0
Lancelets		—	—	—	—	—	—	—	—	—	3.0	—	—	—	—
Fishes		87.0	27.7	24.4	52.3	76.5	82.9	9.1	55.9	0.1	17.0	0.9	—	—	—
Animal fragments		3.2	—	8.0	1.5	8.9	—	—	—	8.2	9.9	10.4	9.4	0.9	8.4
Detritus		5.7	—	0.8	1.5	—	—	—	—	62.4	37.6	8.4	9.3	2.6	8.7
Sand		—	—	—	—	—	—	—	—	1.4	12.6	3.3	—	—	—
Number examined		126	11	9	31	35	38	5	25	103	17	136	47	12	12
Number empty		27	6	1	13	6	18	3	8	53	9	17	24	4	6
Mean weight/stomach (g)		0.051	0.035	0.664	0.353	0.036	0.149	0.058	0.450	0.007	0.012	0.017	0.021	0.058	0.024
Length range		51-139	33-74	152-225	163-250	92-145	92-149	153-173	150-172	75-99	100-159	83-121	95-124	126-152	125-159

age-I silver seatrout from 7-17 m waters, indicating shrimps as the primary food, were based on only two stomachs. Age-I silver seatrout from 18-44 m depths consumed relatively large proportions of squids and stomatopods, unlike any other age/depth category. The most often noted prey taxa in silver seatrout stomachs were *Anchoa* and unidentified caridean shrimps.

Atlantic croaker, hardhead catfish, and longspine porgy were benthic feeders. No significant correlations in diet were found among the four age/depth categories of Atlantic croaker. Although the

TABLE 2.—Stomach contents of hardhead catfish, longspine porgy, and Atlantic cutlassfish collected from Texas coastal waters between 4 June and 3 July 1981, expressed as percentages of total food dry weight by age and depth of capture. A "+" indicates presence in the diet but <0.1%. Fish lengths are mm SL, except Atlantic cutlassfish which are mm TL. Depth ranges are in meters.

		Hardhead catfish				Longspine porgy				Atlantic cutlassfish	
Stomach contents	Age:	0		I		0		I		0	I
	Depth:	7-17	18-44	7-17	18-44	18-44	45-73	18-44	45-73	7-73	7-73
Nematodes		—	0.1	—	0.9	0.2	—	0.2	—	—	—
Polychaetes		4.5	+	—	—	33.0	60.9	47.0	45.6	0.6	—
Bivalves		0.7	—	—	—	0.1	—	—	—	—	—
Gastropods		—	—	—	—	—	6.4	—	—	—	—
Squids		—	—	—	—	—	—	—	—	—	28.8
Copepods		0.2	—	—	—	4.0	4.9	0.2	—	—	—
Stomatopods		0.1	40.1	38.0	85.7	0.6	—	1.3	—	—	0.1
Mysids		—	—	—	—	—	—	—	—	0.8	—
Cumaceans		0.1	—	—	—	—	—	—	—	—	—
Amphipods		—	—	—	—	0.7	—	1.0	3.2	—	+
Crabs		34.1	26.4	29.9	1.1	0.8	3.7	15.7	6.8	0.6	—
Shrimps		37.8	11.2	0.9	12.2	6.7	3.2	4.9	12.7	1.6	0.8
Holothurians		10.0	3.5	11.8	—	—	—	—	—	—	—
Tunicates		—	2.8	—	—	—	—	—	—	—	—
Fishes		1.6	—	9.0	—	1.0	—	2.3	—	81.3	66.6
Fish bones/scales		1.2	9.3	0.5	—	—	—	—	—	—	—
Animal fragments		7.6	2.5	—	—	25.6	7.8	11.0	15.7	10.5	1.3
Detritus		1.9	4.0	9.9	—	25.9	13.2	12.7	16.1	3.4	2.3
Sand		0.5	—	—	—	1.5	—	3.6	—	1.1	—
Number examined		24	13	7	3	127	8	13	42	5	33
Number empty		1	0	1	0	67	0	7	28	2	13
Mean weight/stomach (g)		0.157	0.323	0.967	0.785	0.007	0.005	0.018	0.003	0.070	0.399
Length range		137-192	169-192	202-255	222-255	25-74	40-51	84-94	78-127	229-399	400-595

TABLE 3.—Spearman rank correlation coefficient matrices comparing age and depth-specific diets within species of Texas coastal fishes collected between 4 June and 3 July 1981. Significant correlations indicated by * at 0.05 or ** at 0.01 levels. Depth ranges in meters.

	Age		0		I	
Species		Depth	7-17	18-44	7-17	18-44
Sand seatrout	0	7-17	—	0.215	0.831**	0.847**
		18-44		—	0.484	0.516
	I	7-17			—	0.940**
Silver seatrout	0	7-17	—	0.687*	0.605	0.371
		18-44		—	0.746	0.732
	I	7-17			—	0.555
Hardhead catfish	0	7-17	—	0.186	0.232	0.131
		18-44		—	0.689*	0.697*
	I	57-17			—	0.545
Atlantic croaker	0	7-17	—	0.460	0.346	0.389
		18-44		—	0.569	0.482
	I	7-17			—	0.135

	Age		0		I	
Species		Depth	18-44	45-73	18-44	45-73
Longspine porgy	0	18-44	—	0.590*	0.762**	0.758**
		45-73		—	0.469	0.741*
	I	18-44			—	0.655*

favored prey in three of four categories, polychaetes comprised more than half the diet only in age-0 Atlantic croaker in shallow waters. Age-I Atlantic croaker in shallow waters preferred crabs (mainly *Albunea*). Alpheid and other caridean shrimps formed one-third of the age-0 Atlantic croaker diet in 18-44 m waters, while age-I individuals at these depths consumed large amounts of tunicates. The prey of hardhead catfish was mainly stomatopods, crabs, and shrimps. The diets of age-I hardhead catfish in both inhabited depth ranges were correlated with the age-0 diet in 18-44 m, where the primary food was stomatopods. Age-0 hardhead catfish in shallow waters did not consume stomatopods but concentrated on crabs and shrimps. Crabs comprised at least 25% of the diets of all age/depth categories except the age-I hardhead catfish from 18-44 m depths, probably due to the small number of stomachs (3) analyzed. Identifiable prey taxa were mainly brown shrimp, *Penaeus aztecus*; rock shrimp,

Sicyonia sp.; and the crabs *Albunea* and *Pinnixa*. All comparisons of longspine porgy diets were significantly correlated, except between age-0 in 45-73 m waters and age-I in 18-44 m waters. Polychaetes were the primary food in all age/depth categories, and animal fragments and detritus were also abundant. The main differences between age classes were that age-0 longspine porgy consumed more copepods but less crabs than age-I individuals.

Discussion

The major foods identified in this study are generally similar to the foods of these seven species described by other investigations in the Gulf of Mexico. Gunter (1945), Knapp (1949), and Darnell (1958) reported that hardhead catfish consumed crabs, shrimps, and detritus in estuaries, but provided neither age nor habitat-related analyses of their data. Divita et al. (1983), using samples collected at the same time as ours but analyzing diets by percent frequency of occurrence, reported differences between age-0 and age-I hardhead catfish diets in 9-17 m waters. They found that, in comparison with age-0 individuals, age-I fish consumed holothurians, fishes, bivalves, shrimps, and detritus more frequently and crabs, stomatopods, and polychaetes less frequently. Our results (based on percent dry weight) contrast in that, for the age-I catfish diet, shrimps were less important and stomatopods were more important than in the age-0 diet in 7-17 m waters.

Two studies have investigated the diet of longspine porgy, the results of which generally agree with ours. Henwood et al. (1978), summarizing data over a 130 m depth range and ages 0 and I, found polychaetes, shrimps, and crabs were the most abundant foods. Rogers (1977) analyzed longspine porgy diets in four arbitrary size classes (two each in ages 0 and I) and three arbitrary depth zones (3-18, 19-55, and 56-200 m), but not by age/depth combinations. He found that both ages preferred polychaetes and that age-0 porgy stomachs contained more animal fragments and detritus than did age-I porgy stomachs, as we report. In contrast, though, Rogers noted that age-I longspine porgy preyed extensively on fishes causing midshelf diets to differ from outer shelf diets. The differences between our reports are probably due to Rogers' year-round sampling over a wide area (Texas, Louisiana, and Mississippi shelf).

The diets of sand and silver seatrouts were also examined by Rogers (1977). His three size classes of sand seatrout were all age-0 fish (26-100 mm SL) which consumed fishes, shrimps, and squids, preyed mainly upon fishes in shallow waters and squids in moderate depths, thus agreeing with our data. His largest size class of silver seatrout (76-175 mm SL, ages 0 and I combined) was piscivorous and is comparable to our findings, but no age/depth data were given.

We found the Atlantic croaker diet was influenced by both age and depth of capture. This is the likely reason for the variety of primary foods previously reported for this species. Chen (1976) examined age-0 and age-I Atlantic croaker (data summed over 9-73 m depths) and reported similar diets of primarily organic and inorganic matter with lesser amounts of crabs, shrimps, and stomatopods. Although the influence of depth was not discussed, she proposed that diet variations were substrate-related. Rogers (1977) noted that polychaetes and stomatopods were the main foods of age-0 Atlantic croaker in shallow and moderate depths. Overstreet and Heard (1978) documented both size and depth of capture as factors independently affecting Atlantic croaker diets: small individuals (76-195 mm SL) consumed more polychaetes and fewer molluscs, crustaceans, and fishes than did large individuals (200-351 mm), and fish from shallow water (11-29 m) consumed more polychaetes and fishes and fewer crustaceans than fish from deep water (30-90 m). However, their comparisons apparently included two age classes in each size range, formed arbitrary depth zones, and did not examine age/depth as a combined influence. Divita et al. (1983) found detritus to be the most frequently observed item in both age-0 and age-I Atlantic croaker stomachs from both shallow- and midshelf, and observed no differences in diets among age/depth categories. The available data thus indicate that Atlantic croaker are highly opportunistic in their feeding strategy, which is readily influenced by age, depth, season, and, probably, site.

Our results agree with previous reports concerning offshore spot and Atlantic cutlassfish diets. Chen (1976) examined age-I spot from 9-27 m depths and found inorganic and organic matter, polychaetes, and shrimps were the primary foods. Mericas (1981) noted Atlantic cutlassfish were piscivorous from late age 0 into age III.

We conclude that the degree to which age and depth of capture simultaneously affect fish diets depends upon the species examined: Atlantic croaker are highly influenced and longspine porgy are only slightly influenced. This variation between species may have been due to the age/depth distributions of the fishes during the limited collecting period, and thus seasonal collections should be compared. It is also possible that fishes had fed in one depth zone and moved into the adjacent depth zone prior to capture.

We know of no data concerning swimming speeds of the species examined, but an individual moving completely across one depth zone would cover 6-35 km in southern and up to 20-90 km in northern Texas coastal waters.

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LIFE HISTORY OF SPLITTAIL (CYPRINIDAE: *POGONICHTHYS MACROLEPIDOTUS*) IN THE SACRAMENTO-SAN JOAQUIN ESTUARY[1]

The Sacramento-San Joaquin estuary is the largest on the west coast of North America. Because of its comparatively young geologic age, <8,000 yr (Atwater 1979), its fish fauna is a mixture of native freshwater and marine species, to which numerous exotic species have been added in the past 100 yr (Moyle 1976). The ranges of two extant species, the delta smelt, *Hypomesus transpacificus*, and the splittail, *Pogonichthys macrolepidotus*, are restricted to the estuary. Both species are abundant but their biology is nevertheless poorly known, since most fisheries research in the estuary has concentrated on species of major economic importance, especially the introduced striped bass, *Morone saxatilis* (Stevens 1980; Collins 1982).

The fish communities of the estuary are changing, however, as new species are introduced and as conditions change in response to upstream water projects, water diversions, such as increased use of the water for cooling power plants, and pollution. Given the restricted ranges and habitats of these two species (Moyle 1976), their abundance could decline rapidly if environmental conditions become unfavorable for them, possibly making them candidates for listing as threatened species. This paper is concerned with the life history of the splittail, a species of

[1]Contribution No. 351 from the New York State Museum, Albany, N.Y.

interest for reasons besides its status as a potentially threatened endemic: 1) It is consistently one of the most abundant species in many of the brackish sloughs of the estuary (Moyle and Daniels unpubl. data; Caywood 1974), 2) most other cyprinids are exclusively freshwater species, rarely found in brackish waters, 3) its life history patterns reflect adaptation to an environment in which drought and flood occur episodically, and 4) it supports a small but locally important hook-and-line fishery (Caywood 1974).

Methods

Fishes were collected in the Suisun Marsh between January 1979 and January 1982, using 2.5 m otter trawls (mesh at cod end 6 mm bar) and 3 mm bar beach seines. The Suisun Marsh is the largest contiguous tidal marsh on the eastern Pacific coast (Fig. 1). It comprises 34,000 ha of marshland, sloughs, and shallow bays (Moyle et al. 1982a). At each locality, salinity (‰), water temperature (°C), secchi depth, and turbidity were recorded. Standard length (SL) was measured on all fish captured; for most months a random sample of splittail was preserved in 4% formaldehyde solution. In the laboratory, preserved specimens were measured and weighed. Scales were removed from 210 randomly selected fish, from the area above the lateral line, caudad to the posteriormost point of the pectoral fin. These scales were mounted on glass slides and projected on a microfiche reader screen. Measurement and backcalculation follow Tesch (1968). A condition factor ($K = \text{wt}/\text{SL}(3 \times 10^6)$) was calculated for each fish (Tesch 1968). Gonads were removed and weighed; fecundity was determined by weighing three subsamples from each prespawning ovary, counting the number of ova present in each subsample, averaging, and multiplying by total gonad weight. Stomachs were removed; contents were separated, identified, and weighed. When possible, the total length of prey items was measured. In April 1979, fish were collected over a 24-h period for a feeding habit study. Fullness indices (Windell 1968) were calculated for each fish as an indirect measure of activity.

Several statistical techniques were used. One-sided *t*-tests were used to compare means between two groups; one-way analysis of variance was used to

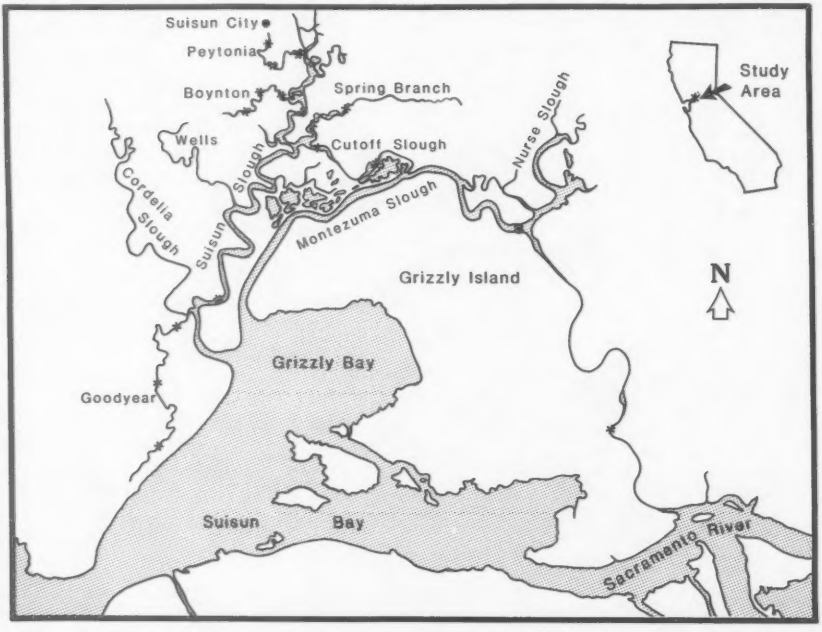


FIGURE 1.—Suisum Marsh, Sacramento-San Joaquin Estuary, Calif. Samples were taken from all sloughs identified. Monthly (1979) or bimonthly (1980-81) sample sites are designated (*). Each site represents two tows.

compare means among three or more groups (Remmington and Schork 1970). Wilcoxon sum of ranks or Kruskal-Wallis tests were used to compare indices (Sokal and Rohlf 1981). Regression lines were compared using techniques in Neter and Wasserman (1974).

Results and Comparisons

Age, Growth, and Condition

Young-of-the-year splittail appeared in samples in late May 1980 and early June 1981 with a mean of 32 mm SL in both years (Fig. 2). Lengths ranged from 23 to 54 mm. The back-calculated length for scale formation was 22 mm. Splittail grew at about 20 mm/mo through September, then that rate decreased to <5 mm/mo through February. In March fish began to grow again and added about 10 mm/mo during the next growing season. During the remaining 3 yr, fish added 5-7 mm/mo in length. These results were corroborated by back-calculating fish length from scales (Table 1). Annuli were formed in March 1979 and in late February 1980 in most specimens. Back-calculated growth rates were similar within the first and second age groups in 1979 and 1980 [age group 0: $F = 2.78 < F_{(0.95;2,12)}$; age group 1: $F = 0.8 < F_{(0.95;2,18)}$] but differed in the third age group [$F = 20.7 > F_{(0.95;2,16)}$]. Growth increments determined from back-calculation also were not significantly different between drought years (1976-77) and wet years (1978-80) in the first two age groups (age group 0: $t = 0.2 < t_{0.95}$; age group 1: $t = 1.0 < t_{0.95}$). These growth rates are similar to those found by Caywood (1974) in the upper Delta. The largest fish encountered in this study was 387 mm SL, which is approximately the

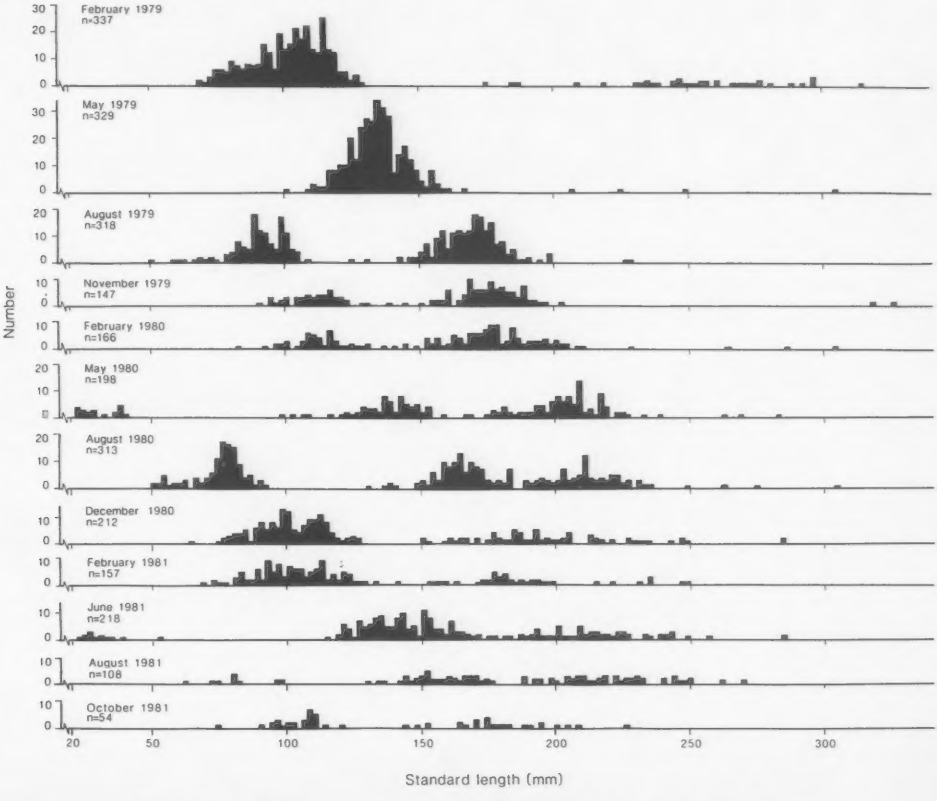


FIGURE 2.—Length (SL) frequency histograms of splittail samples, Suisun Marsh, Calif., 1979-81.

TABLE 1.—Mean back-calculated standard length (mm) and 95% confidence intervals at successive annuli for splittail taken in the Suisun Marsh, Calif., 1979-80.

Age group	n	I	II	III	IV	V
0	11					
1	86	111.8±2.7				
2	56	109.6±4.1	175.3±5.0			
3	29	110.8±4.5	170.2±5.3	218.9±5.0		
4	20	115.7±8.3	162.4±9.0	211.1±6.4	249.7±6.2	
5	8	109.4±12.2	167.3±15.2	213.4±12.4	253.1±14.1	286.8±12.4
Total	210					
$\bar{x}$		111.4	171.2	215.4	250.6	286.8
Increment		59.8	44.2	35.2	36.2	

same maximum size encountered by Caywood (1974). No sex-related differences in growth were detected (t-test, $\alpha = 0.05$).

Monthly mean condition factors of mature fish varied little throughout the year (Table 2). Mean condition factors were significantly higher in females during the months preceding spawning (t-tests, $\alpha = 0.05$); sex-related differences were not significant in other months. The condition factors of immature fish generally were not significantly different from those of mature fish (t-tests, $\alpha = 0.05$). Between-year differences in mean condition factors were not significant in mature fish. However, immature fish of the 1978 year class (immediately postdrought) had mean condition factors significantly higher than those of the 1979 year class in March ($t = 4.81 > t_{0.99}$) and April ($t = 1.73 > t_{0.95}$).

TABLE 2.—Mean monthly condition factors of splittail from Suisun Marsh, Calif., 1979-80. No data are available for December.

Month	Female	Male	Immature
January	23.0	20.4	19.9
February	22.1	21.5	19.7
March	20.5	19.1	20.9
April	20.7	19.6	20.4
May	20.1	17.7	19.5
June	19.2	19.6	19.2
July	19.5	19.9	21.2
August	20.8	19.1	20.2
September	19.8	19.9	19.4
October			18.7
November	21.0	20.5	21.5

Reproductive Biology

Sacramento splittail were mature by their second winter, at minimum lengths of 180-200 mm; both males and females matured at the same age. Caywood (1974), however, noted that a small percentage of the males became sexually mature at the end of their first year and a small percentage of the females did not become mature until their third year. Gonadal growth began to increase in the autumn at about the same time somatic growth declined. Ovaries increased in size until April when they account for 18% of the body weight; testes reached their greatest size in March, April, and May, but never accounted for more than 2% of body weight. Splittail spawned in late April or early May in the marsh. Caywood (1974) found that spawning in the upper Delta occurred between early March and mid-May (in 1973 and 1974). Young-of-the-year fish appeared in our collections in late May or early June at 22-40 mm SL; at this size they had absorbed the yolk sac and were free swimming.

The fecundity (F) of 20 fish > 175 mm SL collected from January through March ranged from 17,500 to 266,000 ova. Mean number of ova per gram body weight (Wt) was 408; in this sample the relationship between number of ova and body weight was $F = 457\ (\mathrm{Wt})^{0.91}$ (log-log transformation $r = 0.546$; $F = 7.64 > F_{1,18}$ at $P = 0.05$). They averaged 600 ova/mm SL. The relationship between fecundity and SL was $F = 0.01\ (\mathrm{SL})^{2.92}$ (log-log transformation $r = 0.536$; $F = 7.25 > F_{1,18}$ at $P = 0.05$). Fecundity increases with length and weight; both adequately predict fecundity.

The onset of spawning appears to be associated with increasing water temperatures and increasing day length; during the spawning period there were no changes in turbidity or salinity. The success of the spawn was correlated with river outflow (Table 3). Caywood (1974) captured ripe splittail in the upper end of a freshwater slough, in association with recently flooded vegetation. It is possible that splittail spawn on vegetation.

Year Class Strength

The percent of each year class in the catch varied (Fig. 3). The 1978 year class was extremely strong and dominant through the 1980 summer. The 1979 year class was never strong and never clearly dominated a monthly sample. Instead it remained

TABLE 3.—Splittail reproductive success, outflows of the Sacramento River at Chipps Island, Calif., and the correlations between them (* = $P < 0.05$, ** = $P < 0.01$). Abundance index is based on the strength of the year class, by percentage of sample (1 = weak, 3 = strong). The index is derived from the collection data of this study, from California Department of Fish and Game unpublished records, and Caywood (1974).

Year	Abundance index	Monthly mean flows at Chipps Island (in cubic feet per second × 10^3)											Annual total
		Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sept.	
1969	3	5	11	26	123	159	94	69	65	47	13	12	20	644
1970	2	19	20	46	193	111	56	11	11	6	5	8	15	501
1971	2	13	26	85	64	34	32	37	26	21	12	13	20	383
1972	1	14	14	24	21	22	18	7	5	3	6	6	10	150
1973	2	12	26	27	11	102	77	22	12	7	5	6	11	318
1974	3	14	60	76	139	59	78	109	26	17	9	13	21	621
1975	2	19	24	28	17	57	67	35	29	23	11	10	13	333
1976	1	17	18	20	9	7	8	9	4	4	4	5	3	108
1977	1	4	4	4	4	5	3	3	4	3	3	3	3	43
1978	3	2	4	9	64	54	84	60	41	9	4	6	12	349
1979	2	10	11	9	30	44	37	14	13	5	5	4	5	187
1980	3	8	12	19	118	122	99	29	21	15	11	4	10	468
1981	1	6	5	12	13	20	21	10	9	5	5	2	4	112
Correlation of flow with index		−0.215	0.316	0.285	0.655*	0.720**	0.924**	0.786**	0.765**	0.600**	0.553*	0.511	0.682*	0.864**

relatively constant, representing 30-50% of the catch. The 1980 year class did not begin to dominate monthly samples until the disappearance of the 1978 year class in November 1980. The 1980 year class remained dominant from that date to the end of the study. The importance of the 1978 year class was indicated by the significant negative correlation ($P < 0.01$) between catch per minute and number of months that had elapsed since the beginning of our study.

Data for 1969 through 1974 from Caywood (1974) and for 1972 through 1978 from the California Department of Fish and Game (CDFG) (D. Kohlhorst unpubl. data) also show strong and weak year classes in splittail. These data sets are not strictly comparable with ours because different methods were used to capture the fish and because Caywood's samples were not from the Suisun Marsh. However, the consistency of the patterns in the data from two sources on the same years (1972-74, 1977-78) allowed us to rank year class strength from weak to strong, on a 1 to 3 scale (Table 3). Although the use of such a scale is likely to bias an analysis against finding significant correlations (Thorndike 1978), strong positive correlations ($P < 0.01$) were nevertheless found between year class strength and outflows in February, March, April, and May, as well as with total outflows. Splittail may spawn on flooded vegetation in March and April. Thus, wet years, such as 1974 and 1978, show extremely large year classes that remained abundant for several successive years. During drought years, such as 1976 and 1977, nearly complete year class failures occurred. CDFG collected only one young-of-the-year in 1976 and none in 1977. Our samples in January-March of 1978 yielded only large adults, none of which was from the 1976 or 1977 year classes.

Feeding

Splittail prey upon a variety of organisms but detritus dominates gut contents (Table 4). A small part of the gut content was unidentifiable animal matter. *Neomysis mercedis* was the dominant prey item, and crustaceans accounted for almost 85% by volume of the animal portion of the diet. *Neomysis mercedis* dominated the diet seasonally and through a diel cycle. Annelids, molluscs, insects, and fish completed the prey list; all were relatively unimportant components. These results are in contrast to those of Caywood (1974) who analyzed three collections of splittail from the upper Delta. He found the dominant animal matter in the stomachs to be clams (*Corbicula manilensis*), amphipods (*Corophium* spp.), copepods, and dipteran larvae and pupae. In a sam-

TABLE 4.—Prey items taken by 635 splittail collected from the Suisun Marsh, Calif., 1979-80.

Item	Frequency of occurrence (%)	Volume (%)	Volume less detritus/substrate (%)
Detritus/substrate	74	57	—
Polyclads	1	<1	<1
Polychaetes	3	2	3
Oligochaetes	1	<1	1
Molluscs	1	<1	<1
Crustaceans		35	
Harpacticoid copepods	15		7
Other copepods	7		2
Ostracods	6		<1
Cladocerans	1		1
Corophium	8		9
Other amphipods	1		2
Isopods	<1		1
Neomysis	37		59
Crangon	3		1
Palaemon	<1		<1
Insects		1	
Collembola	1		<1
Coleoptera	1		<1
Diptera	1		<1
Fish	1	2	3
Unidentified	6	3	7

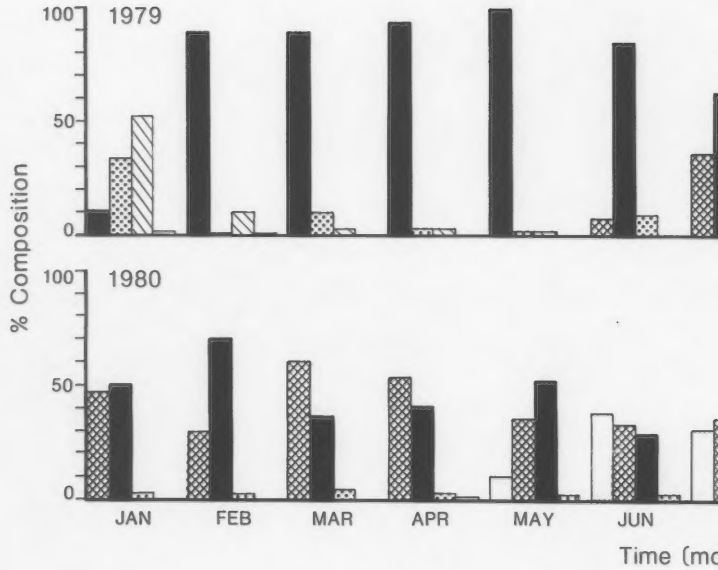
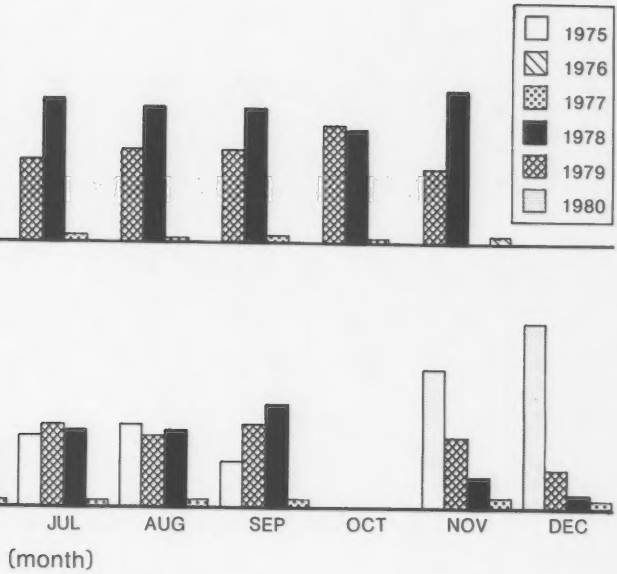


FIGURE 3.—Year class strength of splittail as percentage of



age of sample, Suisun Marsh, Calif., 1979-80.

ple of splittail taken in a flooded pond, however, the main food was earthworms (*Lumbricus* sp.). The types of prey consumed indicate that splittail are bottom feeders. Feeding activity, inferred from fullness indices, was greatest during morning and early afternoon. The mean fullness index for fishes collected from 0600 to 1400 was 5.4, the mean index for fishes collected at 1800 and 2200 was 2.3. There was a seasonal difference in fullness indices of fishes collected midday (Kruskal-Wallis $\chi^2 = 28.9 > \chi^2_{0.99}$). The greatest mean index (2.8) was calculated from fishes collected during the summer. Mean autumn, winter, and spring indices ranged from 1.3 to 1.8.

Discussion

Sacramento splittail is a major component of the Sacramento-San Joaquin estuary fish association. Although abundant within its range, Sacramento splittail is now confined to the lower Delta and the main channel of the Sacramento River, a fraction of its former distribution (Moyle 1980). Population size fluctuates drastically from year to year and year class strength varies annually.

Within the Suisun Marsh, Sacramento splittail is dominant, by number, in the small cul-de-sac sloughs where it is associated with other native fishes (Moyle et al. 1982b). It is a benthic feeder with a limited range of prey types. *Neomysis mercedis*, the primary, nondetritus/substrate component of its diet, is abundant throughout the marsh and serves as a major food source of most other fishes in the marsh as well (Moyle and Daniels unpubl. data).

Sacramento splittail grows to moderate size, lives a relatively long life, and produces a large number of eggs per year. This is typical of native California cyprinids, particularly those found in the larger rivers and lakes (Moyle et al. 1982b). Such a pattern allows this annual spawner to fail to reproduce during environmentally unfavorable years. Unfavorable conditions, which, in the case of splittail, may include high salinities, low water levels, and/or high temperatures, are (or were) periodic and predictable. Particularly dry years occurred in 1972, 1976, and 1977. During these years splittail either failed to spawn or the spawn failed to develop; however, adults were present in the sloughs. A similar relationship between year class strength and outflows has been demonstrated for striped bass for the years 1959-76, although since then the relationship has not been as strong (Stevens 1980).

The small shallow sloughs lined with emergent vegetation inhabited by splittail offer protection from larger piscivorous fish and provide abundant sources of food. The periodic fall in water level simultaneously concentrates prey in the remaining shallow water and excludes large predatory fishes. Avian and mammalian predators are thwarted in all but the most shallow water by its turbidity.

Tolerance to relatively high salinities is unusual in cyprinids although tolerances similar to that of splittail have been recorded for carp, *Cyprius carpio*, and peamouth, *Mylocheilus caurinus* (Scott and Crossman 1973). It is likely that salinity tolerance in splittail increases somewhat with size, as many large (200 mm SL+) adults were collected from the more saline areas (>8‰).

Acknowledgments

In a project that lasts many years and includes over 100 sampling days, many people are responsible for its success. We thank all the individuals, mostly volunteers, who helped in the field. We are particularly grateful to D. M. Baltz, B. L. Herbold, and L. M. Brown for continued assistance in the field and laboratory and for reviewing the manuscript. We also thank R. L. Brown, who was instrumental in securing the resources necessary to complete this project, and D. Kohlhorst of CDFG, who allowed us to examine and report unpublished information collected over a 7-yr period. This work was supported by grants from the California Department of Water Resources.

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LIFE HISTORY AND EXPLOITATION OF *MACROBRACHIUM FAUSTINUM* IN A TROPICAL HIGH-GRADIENT RIVER

Macrobrachium spp. are widely distributed in tropical freshwaters where they often support commercial or artisanal fisheries (Holthuis and Rosa 1965; Holthuis 1980). Studies of exploited *Macrobrachium* stocks have been carried out in large, low-gradient rivers in Liberia (Miller 1971), India (Rajyalakshmi and Ranadhir 1969), and the Philippines (Rasalan et al. 1969), but do not provide the bionomic information necessary for a quantitative assessment of the response of the stocks to exploitation. We know of no such study of a wild population of *Macrobrachium* species.

Macrobrachium faustinum inhabits freshwaters throughout the Caribbean area and in Florida (Chace and Hobbs 1969). In Jamaica it is the most common, eurytopic, freshwater shrimp, inhabiting both slow-flowing rivers and marshes in low lying areas, and fast-flowing streams in hilly regions (Hunte 1978). In the former, *M. faustinum* supports trap fisheries; in the latter it is fished either by hand or by turning over stones and allowing the shrimps to be washed into baskets. Although this fishery is pursued part time by children and men after work, these and other shrimps from small rivers are an important dietary component in an area where protein is scarce and expensive. In this paper we describe the bionomics of *M. faustinum* in a high-gradient stream (Cane River, Jamaica), and assess the effects of fishing on yield and population fecundity.

Description of Study Area

Cane River (lat. 17°58'N, long. 76°44'W) flows into the Caribbean Sea on an exposed south shore (Fig. 1). There is no protected bay at the river mouth, and the estuary is small. Altitude at the source is about 650 m, total length about 10.2 km, overall mean width 2.3 m, and mean depth about 9.4 cm. The width and depth vary markedly with seasonal rainfall. Cane River is a characteristic high-gradient stream in Jamaica. The water is clear and fast-flowing with a high oxygen content and a rocky bottom devoid of macrovegetation. Mean oxygen concentration along the river was 8.5 mg/l, mean pH 7.3. Mean temperature at the extreme lower limit of the river was 25.4°C with a mean daily range of 8.6°C and a mean seasonal range of 4.2°C. Corresponding temperature values at the extreme upper limits were overall mean 21.7°C, mean daily range 3.7°C, and mean seasonal range 3.4°C. The river bed consisted of stones, pebbles, gravel, sand, and mud over rock.

Materials and Methods

Shrimps were collected using a combined Surber sampler (Moffett 1936; Surber 1936) and Box sampler (Berg 1938). It consisted of a square frame of 0.25 m^2 with four legs protruding 5 cm below the frame and 40 cm above it. Net (1 mm square mesh) enclosed the sampler on three sides. Flaps of net under all four sides of the frame served as a seal between the frame and the substrate. On the fourth (downstream) side, there was a detachable collecting net 80 cm long with a mouth 50 × 40 cm (1 mm square mesh).

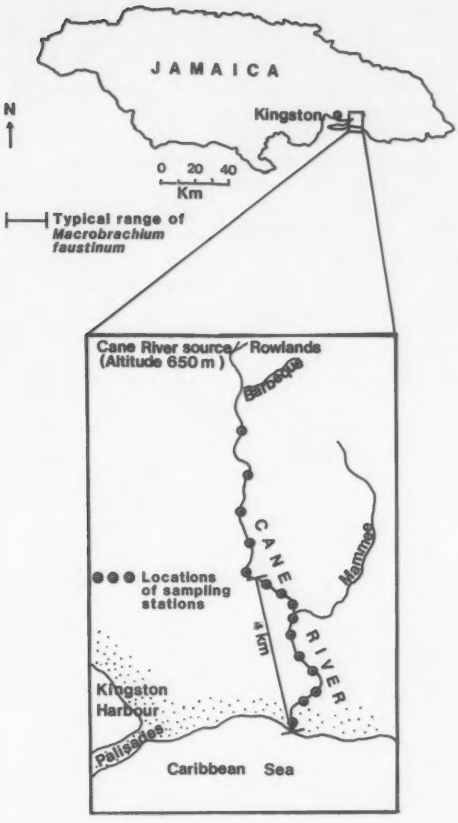

FIGURE 1.—Map of study area and its location in Cane River, Jamaica.

To sample, the legs were forced into the substrate and the net flaps pinned around by stones. The collecting net was attached to the frame, and its bottom side held firmly down by the operator's feet. All stones within the sample area were then removed and the shrimps swept into the collecting net by the current.

During a 20-mo period (February 1973-September 1974), 10 samples, randomly chosen, were taken monthly at each of 15 stations along the length of the river. Areas of the stream bed which were devoid of stones were not sampled since they were known to be without shrimps (Hunte 1976). Samples were taken during the day when the shrimps are inactive and hide under stones.

Each specimen of *M. faustinum* was sexed, and its total length measured (from the tip of the rostrum to the tip of the telson) to the nearest 0.5 mm for adults and 0.1 mm for juveniles. Specimens subsampled from each month's catch were weighed to the nearest 10 mg for adults and the nearest 1 mg for juveniles. Growth and mortality were estimated from monthly length-frequency histograms.

The catch of fishermen was sampled opportunistically throughout the period of sampling in the river. On each occasion the shrimps in the catch were measured and the resulting length-frequency distribution converted to a catch curve using the age-length relationship.

Yield per recruit (Y/R) for various levels of fishing mortality (F) was estimated for males and females combined by the method of Thompson and Bell (Ricker 1975), using an APL algorithm (Rivard 1980). The parameters required for the input are b, age of the youngest age-group fished; m, age of the oldest age-group fished; w_i, weight (g) at age i; r_i, the partial recruitment to fishing mortality at age i; and M, the instantaneous rate of natural mortality. Then

$$Y/R = \sum_{i=b}^{m} w_i N_i F_i \frac{(1 - e^{-Z_i})}{Z_i},$$

where $F_i = r_i F$, $Z_i = F_i + M$, and $N_i = N_{i-1}\, e^{-Z_{i-1}}$. The sequence of N_i for each age-group in the fishery is calculated assuming $N_b = 1$.

The partial recruitment to fishery mortality (r_i) is the proportion of the fishing mortality which can be allocated to age-group i. These values increase throughout recruitment to a maxium of 1 for fully recruited age-groups. In this study r_i was estimated as the ratio of the proportions of age-group i in the catch and population survey, standardized to a maximum of 1 by dividing each ratio by the largest one (Winters 1978).

The number of eggs produced per female recruit (E/R) was estimated for various levels of fishing mortality.

$$E/R = \sum_{i=a}^{m} E_i N_i$$

where a is the age of first maturity for females and E_i is the number of eggs per female at age i. For postrecruits ($i > b$), N_i were as defined above for the estimation of Y/R. For prerecruits ($i < b$), N_i were backcalculated assuming $N_b - 1$, and $Z = M$. The number of eggs per female at each age was determined from the fecundity-length and age-length relationships.

Results

Cane River does not flow through to the sea for much of the year (January-August). As the larvae of *M. faustinum* must develop in the sea (Hunte 1980a, b), juveniles enter the river during a short period each year. Consequently, length-frequency histograms showed distinct modes which were useful for growth and mortality analyses (Fig. 2).

Juveniles entered the river between September 1973 and January 1974, and again in September 1974 (Fig. 2). The weighted mean time of entry of the 1973 cohort was in early December, and was assumed to be early December for all cohorts. At this time shrimps were about 3 mo of age. The peak of the breeding season is about 3 mo earlier (see Fig. 4). Larval development in the laboratory takes about 95 d (Hunte 1980a) after which the length of the juveniles (Hunte 1980b) is similar to that of juveniles entering the river.

Monthly growth for males and females (Fig. 3) was estimated from changes in mean length of cohorts (Fig. 2). Sex could not be distinguished before about 10 mo, when all members of a cohort are longer than 20 mm. Males grew slightly faster than females (Fig. 3).

The wet weight/length relationship for males was $\log W = 3.15 \log L - 2.02$, and for females $\log W = 3.23 \log L - 2.20$. The regression coefficients do not differ significantly, but are significantly >3, indicating allometric growth ($b > 3$; for males $t = 2.64$, $P < 0.01$; for females, $t = 5.14$, $P < 0.001$).

Females composed 49% of adult shrimps caught (i.e., those >20 mm). This was not significantly different from a 1:1 sex ratio ($\chi^2 = 0.81$, $P > 0.25$).

No females smaller than 26 mm (about 9 mo old) bore eggs. This is therefore an estimate of the minimal size (age) at sexual maturity. Of the females in the 26-28 mm size class, 39% were berried, compared with 51% for all mature classes combined. This suggests that most females mature in the 26-28 mm size range, with little variation in size at sexual maturity.

Eggs were oval, about 0.54 by 0.42 mm when laid, and about 0.70 by 0.53 mm prior to hatching. Egg size was independent of female length. Eggs were counted on females carrying eggs in advanced developmental stages, and the fecundity/length relationship was $\log F = 3.52 \log L - 2.47$.

Monthly percentages of mature females carrying eggs (berried) showed that spawning was continuous but peaked between June and November (Fig. 4), just before or during the months of heaviest rainfall in Jamaica.

Total mortality for the *M. faustinum* stock is estimated from the decline in monthly catch of the four year classes sampled in this study (Fig. 5). The percentage contribution of each age-group to the fishermen's catch shows the age of first capture to be 16 mo and full recruitment to the fishery to be at 24 mo (Fig. 4). There is a distinct increase in mortality at, or just before, the age of complete recruitment. We estimate the instantaneous rate of natural mortality (M) as equal to the instantaneous rate of total mortality (Z) for the prerecruits (ages 5-15 mo). Fishing mortality (F) is taken as equal to Z-M for the fully recruited age groups (25-34 mo). The estimates of M and F are 0.13 and 0.15, respectively, and the former is used in the estimation of Y/R.

The information used to calculate the partial recruitment values is given in Table 1. The ratios of proportion in catch to proportion in the survey indicate that F increases steadily with age and size. However, as there are relatively few individuals in the older age-groups, we felt it more appropriate to consider recruitment as complete at age 24 and to assign $r_i = 1$ to all older age-groups. Therefore, all values of r_i for $i < 24$ are relative to the catch survey ratio at age 24.

The relationship between Y/R and F (Fig. 6) appears to be asymptotic; therefore, no F for maximum yield could be computed. However, beyond an F of about 0.5 the returns in terms of Y/R for increased F are minimal. Both the mean weight of shrimp in the catch and the index of catch per unit effort change most rapidly at values of F less than about 0.5.

The relationship between fishing mortality and the number of ripe eggs produced per recruit shows that

TABLE 1.—The calculation of partial recruitment to fishing mortality at each age for *Macrobrachium faustinum* in Cane River, Jamaica.

Age (months)	Percent in catch	Percent in survey	Ratio catch/survey	R_i used in Y/R estimates
16	1.1	10.0	0.11	0.048
17	1.1	10.1	0.11	0.048
18	3.2	10.7	0.30	0.130
19	2.3	9.8	0.23	0.100
20	5.9	8.6	0.69	0.300
21	3.6	7.3	0.49	0.210
22	9.0	6.7	1.35	0.59
23	11.1	6.7	1.66	0.72
24	14.7	6.4	2.30	1
25	9.5	5.6	1.70	1
26	6.5	4.7	1.38	1
27	6.1	3.8	1.60	1
28	6.1	2.8	2.18	1
29	5.3	2.2	2.41	1
30	2.3	1.4	1.64	1
31	3.8	1.3	2.92	1
32	3.4	0.9	3.78	1
33	3.4	0.7	4.86	1
34	1.9	0.3	6.33	1

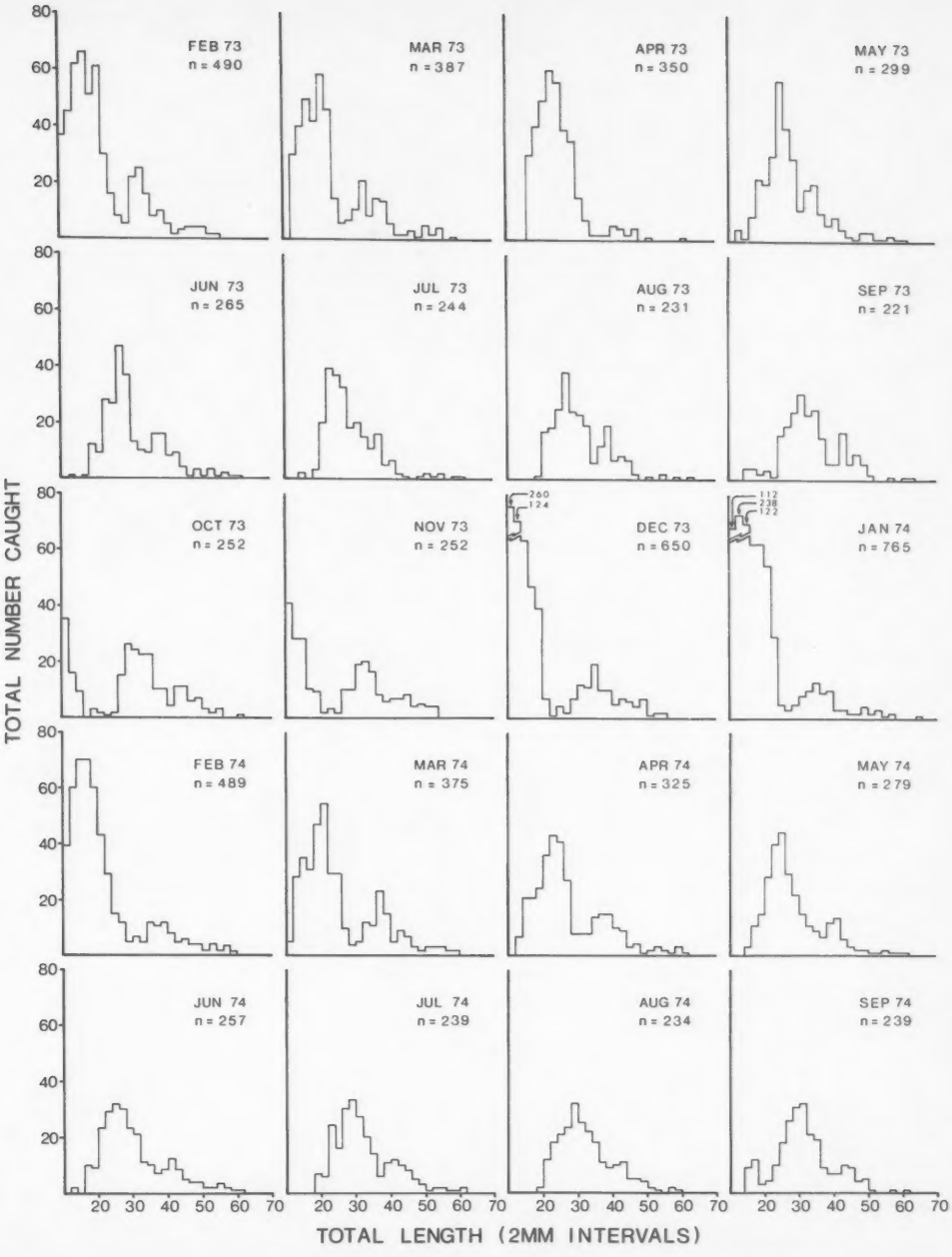

FIGURE 2.—Monthly length-frequency histograms for *Macrobrachium faustinum* in Cane River.

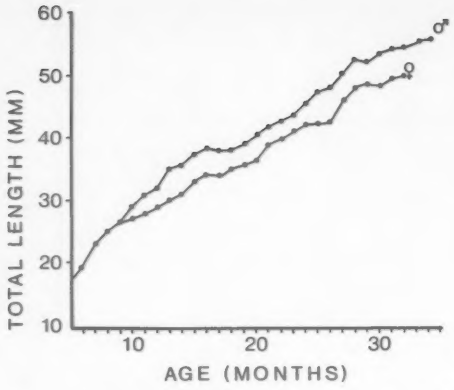

FIGURE 3.—Growth of *Macrobrachium faustinum* in Cane River.

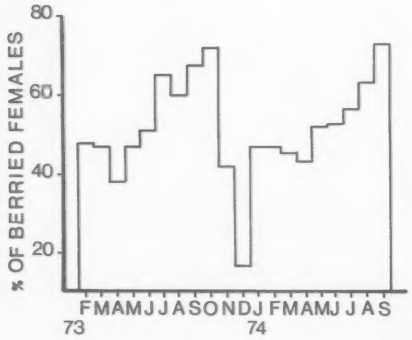

FIGURE 4.—Seasonal variation in the percentage of berried *Macrobrachium faustinum* in Cane River.

even at relatively high values of fishing mortality ($F = 2.0$) egg production is only 37% less than at $F = 0.1$ (Fig. 7).

Discussion

Macrobrachium faustinum and other small shrimps support important subsistence fisheries in the hilly regions of Jamaica and throughout the Caribbean. Management of a resource so widely and diffusely distributed throughout the countryside is difficult. Consequently, to assess the need for management it is important to have some understanding of the likely effects of increased exploitation on these shrimps.

The asymptotic relationship between Y/R and fishing mortality suggests that the shrimps are unlikely to be overfished from the viewpoint of optimal yield of biomass. At the present level of fishing mortality ($F = 0.15$) there would be substantial gains in yield from small increases in fishing effort (Fig. 6). However, sharp reductions in catch per unit effort and in the mean size of shrimp captured would be expected to accompany increased exploitation. *Macrobrachium faustinum* is already small, and we expect that, except in the event of extreme food shortage, the reduction in mean size and catch per unit

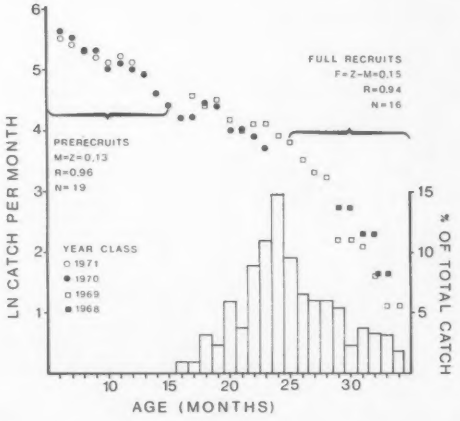

FIGURE 5.—Mortality of *Macrobrachium faustinum* in Cane River as indicated by decline in abundance of year classes (catch per month), and the age composition of the fishermen's catch (percent of total catch).

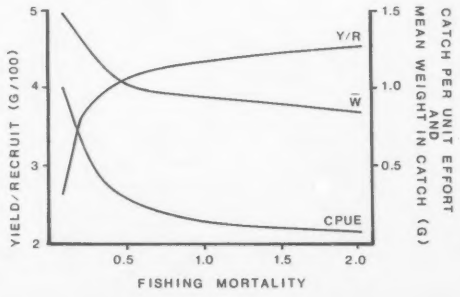

FIGURE 6.—The relationship of yield per recruit (Y/R), mean weight of shrimp caught ($\bar{w}$), and the index of catch per unit effort (CPUE) to fishing mortality for *Macrobrachium faustinum* in Cane River.

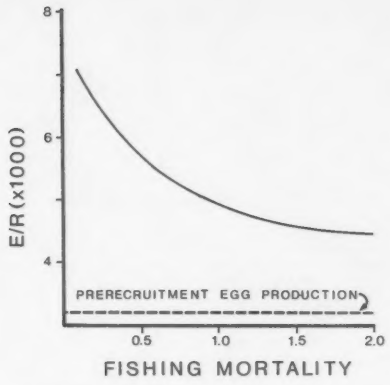

FIGURE 7.—The relationship between fishing mortality and the number of eggs produced per recruit for *Macrobrachium faustinum* in Cane River.

effort of shrimp will self-regulate the fishery. The low level of F suggests that this effect is currently operative.

Even though yield (growth) overfishing is unlikely, the possibility of recruitment overfishing (Cushing 1977) must be considered. This too is unlikely, because *M. faustinum* mature early and a high proportion of egg production takes place before recruitment to the fishery (Fig. 7).

Animals which are small, highly fecund, and mature early are to be expected in a habitat where density-independent mortality prevails and is not stronger and/or more variable for juveniles than for adults (see Stearns 1977). In the rainy season Cane River is subject to flash floods which cause high density-independent mortality of shrimps (Hunte 1976). This is almost certainly true of all high-gradient streams in the Caribbean and the shrimps which inhabit them would be expected to have life history characteristics similar to *M. faustinum*. It appears likely then that such species, many of which support significant subsistence fisheries, will be resistant to overexploitation and that regulatory management need not be considered.

Acknowledgments

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INCIDENTAL CATCH OF HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.), IN HERRING WEIRS IN CHARLOTTE COUNTY, NEW BRUNSWICK, CANADA

In this report we examine the indirect exploitation of harbor porpoises, *Phocoena phocoena*, by the weir fishery for herring (*Clupea harengus*) in Charlotte County, New Brunswick, in the lower Bay of Fundy. This fishery is of considerable economic importance to the region; the landed value averaged 2.2 million dollars annually from 1974 to 1979 (table 11 in Iles 1979). Although herring constitute 50% of the harbor porpoise diet (Smith and Gaskin 1974), the level of competition and conflict between *P. phocoena* and the fishery is unknown.

The harbor porpoise is taken accidentally by several commercial fisheries throughout the world (Mitchell 1975), including a pound net fishery in Denmark (Andersen 1974) similar to the weir fishery of eastern Canada. In Canadian waters, harbor porpoises have been caught frequently in Newfoundland cod traps (Sergeant and Fisher 1957) and an unknown number are killed annually in gill nets in the Gulf of St. Lawrence (Laurin 1976). In addition to the indirect catch in the Bay of Fundy, harbor porpoises have been hunted for food and oil by native people and fishing families from at least the 19th century to the present (Gilpin 1878; Leighton 1937; Prescott et al. 1981). An unknown number of animals were also used as mink food in the 1950s (Fisher and Harrison 1970).

As part of a continuing study of *P. phocoena*, we had the opportunity to examine 48 specimens trapped in herring weirs since 1969. Eleven were tagged or equipped with radio-telemetry packs and released (Gaskin et al. 1975). The remainder were routinely autopsied and ages of 30 specimens were estimated from dentinal growth layers (Gaskin and Blair 1977).

Since no formal reporting system exists, we attempted to assess the annual rate of entrapment by mailing questionnaires to all 214 members of the Fundy Weir Fishermen Association in 1980. A total of 49 questionnaires were returned, of which 36 (16.8%) were of a usable nature.

Specimens Examined from Herring Weirs

The 48 harbor porpoises examined between 1969 and 1982 consisted of 22 females and 26 males. Harbor porpoises became trapped in weirs from May to December with the majority (36) taken in July and August. Ages ranged from 0 to 8 yr, with a disproportionate number of 1-yr-old animals. Over half (52%) of the aged sample ($n = 25$) taken from 1969 to 1973 consisted of 1-yr-old harbor porpoises, while yearlings constituted only 18.9% of a sample of 95 animals collected by shotgun from the free-ranging population during the same time period (Fig. 1).

This catch bias may be a consequence of the inexperience of 1-yr-old harbor porpoises in echolocation, navigation, and prey capture. *Phocoena phocoena* has a lactation period of only 8 mo (Gaskin et al. 1981), short in comparison with other odontocete species. Brodie (1969) suggested that prolonged lactation in odontocetes is attributable to the

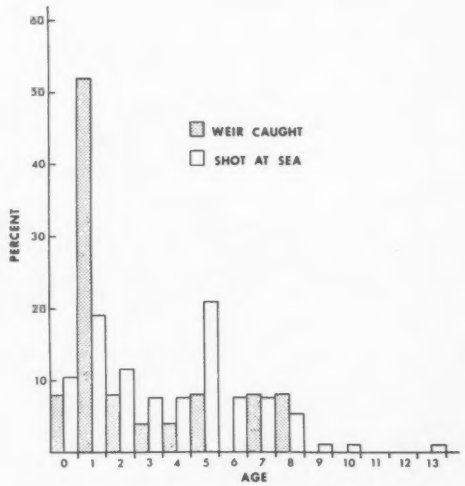

FIGURE 1.—Frequency histogram of age classes (estimated from dentinal growth layers) of harbor porpoises collected in the Bay of Fundy, 1969-73, expressed as percentage of totals captured by two methods: Weir-caught ($n = 25$) and shot at sea ($n = 95$).

sophisticated navigational training required by young animals.

Andersen (1974) concluded, on the basis of parasitic infestation, that about 90% of the 50 harbor porpoises he examined from Danish pound nets were "sick." Most of the yearlings autopsied from our weir sample were only lightly parasitized and appeared to be in good health. Older harbor porpoises were heavily infected with pseudaliid lung worms and campulid liver flukes, but in our experience this is typical of the adult population in general (Arnold and Gaskin 1974).

Many of the harbor porpoises we examined had empty stomachs, indicating either a lack of available fish in the weir or refusal to feed while trapped. Harbor porpoises observed inside weirs usually appeared to be stressed, breathing rapidly and swimming quickly (1.5 m/s) in a regular circular or figure-eight pattern. These animals rarely demonstrated any behavior that might have been interpreted as feeding or foraging activity.

Weir Entrapment Questionnaire

The 36 respondents reported 59 trapped harbor porpoises over the 5-yr period, 1975-79. Of these animals, 23 (39%) were shot or died accidentally, usually by drowning after becoming entangled in the seine net while being removed. The majority of weir fishermen (72%) indicated that they endeavored to release the animals unharmed, either by seining and releasing them, or by waiting for the animals to escape on their own. One respondent who shot entrapped harbor porpoises indicated that the meat was used for human consumption. In general, weir fishermen displayed a favorable attitude towards harbor porpoises, in contrast to their attitude towards harbor seals, *Phoca vitulina*. Harbor seals are generally considered pests, as they swim freely in and out of weirs and may chew holes in the netting.

Fourteen respondents indicated that harbor porpoises became trapped in weirs during the summer months (July-September), while only one reported entrapment at other times (September-October). This is in agreement with our own observations and reflects the seasonal abundance of both harbor porpoises and herring in inshore waters (Gaskin 1977).

Many responses (12 of 18) indicated that harbor porpoises usually entered herring weirs at night. This suggests that visual detection of the weir is important in avoiding entrapment. Busnel et al. (1965) found that a captive harbor porpoise using only echolocation had difficulty avoiding transparent nylon monofilament 3.5 mm in diameter. Since the netting on weirs is constructed from synthetic material, it may not be readily detectable by echolocating harbor porpoises.

Herring tend to be closer to the surface at night than during daylight hours (Brawn 1960) and thus are more susceptible to the weir fishery during this period. Harbor porpoises may follow schools of herring into the weirs and then become trapped. However, questionnaire respondents indicated that large numbers of herring were not always present when entrapment occurred. Some harbor porpoises, therefore, presumably became trapped as a result of foraging on small schools of herring or other prey species.

Impact of the Fishery on the Population

If the annual bycatch per weir (0.328) calculated from the questionnaire returns is representative of all 216 licensed weirs, some 70 harbor porpoises become trapped in Charlotte County each year. Of these animals, 27 die as a result of entrapment.

Gaskin (1977), using uncorrected sighting per unit effort data, estimated the harbor porpoise population in the lower Bay of Fundy as 4,000 during mid-August. Prescott et al. (1981) estimated the August population in the "western half of the Bay of Fundy" as 3,456, using aerial strip census methodology. The annual mortality inflicted on the harbor porpoise population by weirs in Charlotte County would appear to be $<1\%$ of these population estimates. An unknown number of individuals from this population are trapped in weirs in northern Maine (Prescott and Fiorelli 1980) and a few scattered weirs along the Digby, Nova Scotia, shore and in Saint John County, New Brunswick (incomplete data from questionnaire returns).

Subsistence hunting for harbor porpoises is at a very low level in Charlotte County at the present time, although one native hunter claimed to have taken approximately 50 animals in 1979 (Prescott et al. 1981). Based on our own observations, however, native hunters from Maine take only 5-10 harbor porpoises each summer in the area. Harbor porpoises used for human consumption by New Brunswick fishing families are almost invariably from herring weirs or gill nets.

Entanglement in gill nets has a much greater potential for impact on the *P. phocoena* population since there is no opportunity for live release. About 20 fishermen actively gill net in the county (A. B. Cross[1]), but we have little information on the level of

[1]A. B. Cross, Fisheries and Oceans Canada, Lord's Cove, Deer Island, New Brunswick, Canada E0G 2J0, pers. commun. August 1982.

incidental catch. Those interviewed by us reported catching 0-3 harbor porpoises/year. Prescott and Fiorelli (1980) suggested that the incidental catch by gill nets in the Gulf of Maine may be as high as 300 harbor porpoises/year. In Charlotte County, however, the mortality appears to be no greater than that inflicted by the weir fishery.

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A TECHNIQUE FOR TAGGING DEEPWATER FISH

Mark-recapture data have been used extensively in fishery science to estimate population size, survival/mortality rates, growth rates, and movement parameters. Many devices and methods have been used to tag fish (reviewed extensively by Laird and Stott 1978). Virtually all tagging methods necessitate bringing the fish to the surface for marking. For fishes with physoclistic swim bladders inhabiting deeper waters, raising them to the surface subjects them to rapid changes in hydrostatic pressure and, usually, temperature. Procedures used to obtain healthy fish for marking include venting of excess gases from the swim bladder and body cavity with a hypodermic syringe (Gotshall 1964) and raising the fish gradually to the surface to allow acclimatization to changing pressure. Additionally, Phillips (1968) attempted to mark California rockfish by using detachable hooks with "Peterson type" plastic discs fastened to the hooks with wire. However, these methods are at best only moderately successful, as well as time consuming, often expensive, and simply impractical in some situations.

In 1978 we began an investigation of the life history and population dynamics of tilefish, *Lopholatilus chamaeleonticeps*, in the Mid-Atlantic Bight. Reasonable interpretation of these data requires knowledge of tilefish movements. Because tilefish are caught on longlines from depths of 73-254 m along the outer continental shelf (Grimes et al. 1980), fishing operations usually kill or severely injure the fish, thus making conventional marking at the surface pointless. This note describes the design and evaluation of a technique we developed for tagging tilefish, and potentially other deepwater fishes, with tags designed to detach from a bottom longline, thus eliminating the problems of pressure and temperature changes caused by raising fish to the surface.

Methods

We intended to design a tag that could be lightly attached to a longline, so that when a fish took a baited tag the hook would become lodged in the jaw or lip, detach, and thus mark the fish. We designed and constructed tags similar to the snoods or branch lines used on commercial longline fishing gear (see Freeman and Turner 1977 for a description of the gear). These tags consisted of a 30 cm length of 23 kg test monofilament line inserted through red vinyl tubing. We crimped an 8/0 hook to one end of the tag, and the other end was looped, crimped, and attached to the longline groundline at 4 m intervals. No addresses or serial numbers were printed on the red vinyl tubing in these preliminary experiments because our only purpose was to determine if this tagging method was functional. No reward was offered, but tags were returned because we personally alerted most fishermen. This was possible because of the small size of the fishery (i.e., about 25 vessels with most operators already cooperating with our research program by maintaining catch and effort logs) and also because of the localized nature of the tilefish ports (i.e., only two ports landed significant numbers of fish). Because we intended to evaluate only the tagging procedure, we did not request biological data on tagged fish that were caught.

To determine the optimal tag design, we tested different hook types (straight and circle) and different strengths of monofilament (0.9, 1.8, 2.7 kg test) for attaching tags to the longline. The vinyl portion of each tag was knotted to indicate the strength of monofilament (i.e., no knot for 0.9 kg, one knot for 1.8 kg, and two knots for 2.7 kg test).

We attached tags to longlines in two different sequences or "series" (one and ten) of attachment strength and hook type. To prevent a patchy distribution of tilefish from biasing the frequency of removal of tags of various hook types and attachment strengths, the "one-series" tagging consisted of one tag with a particular sequence of attachment strength and hook type (e.g., one 0.9, one 1.8, and one 2.7 kg monofilament with straight hooks; one 0.9, one 1.8, and one 2.7 kg monofilament with circle hooks, etc.). To make identification of hook type and attachment strength easier when we observed tagging longlines from a research submersible, the "ten-series" consisted of 10 tags with a particular sequence of attachment strength and hook type (e.g., ten 0.9, ten 1.8, and ten 2.7 kg monofilaments with straight hooks; ten 0.9, ten 1.8, and ten 2.7 kg monofilaments with circle hooks, etc.).

Longlines fitted with detachable tags were coiled in galvanized tubs, transported to the fishing grounds, and set voluntarily on two occasions by cooperating commercial fishermen. On one tagging operation (at east Hudson Canyon, 23 August 1979, lat. 39°38'05"N, long. 72°16'35"W, 117 m) conducted simultaneously with a gear evaluation study (Grimes et al. 1982a), an onboard observer recorded the numbers of tags of various attachment strengths and hook types remaining on the longline after retrieval. On the other tagging operation (west Hudson Canyon, 17 September 1979, lat. 39°20'30"N, long. 72°26'30"W, 137 m), the longlines were set and retrieved by commercial fishermen who returned the gear for us to

count detached tags. Any tags fouled and detached on deck during setting were retained by the fishermen, returned to us, and counted. Thus our effort between tagging longline sets consisted only of counting detached tags and replacing them with new tags.

The results of experimentally setting tagged longlines (i.e., the variation in proportions of detached tags in relation to various attachment strengths, hook types, tagging locations, and series) were tested by analysis of variance (ANOVA) using the Statistical Analysis System (Barr et al. 1976).

Results and Discussion

A total of 1,156 detachable tags (687 of one-series and 469 of ten-series) were set with various hook types and attachment strengths on two separate occasions near Hudson Canyon (Table 1). Following retrieval of the longlines we determined that 384 detachable tags had been lost, 96 at the east Hudson location and 288 at the west Hudson site (Table 1).

ANOVA of the proportions of tags detached showed significant variations in detachment rate (Table 2). Significant or near-significant probability levels were calculated for variations in proportions of detached tags in relation to the following sources of variation: Tagging location (east or west Hudson); series (one or ten); tagging location-series interaction; attachment strength; hook type; and hook type-tagging location interaction (Table 2).

We know that some accidental tag loss occurred due to fouling, which was observed at the east Hudson site as the gear was being set. However, we believe that detachment rate data actually reflect the relative abundance of tilefish tagged. This is supported by observations made from a submersible at the same time and location (Grimes et al. 1982a); in a transect of commercial longline gear, tilefish were hooked on 42 of 227 hooks (0.19 hooking rate). This hooking rate was nearly identical to the 0.19 loss rate for all tags set at the east Hudson location (Table 3). Evidently, tag loss from fouling was a random event that occurred irrespective of hook type or attachment strength and thus did not affect the analysis, although it could be logically reasoned that weaker attachment strengths and curved hooks would foul most readily.

We know no obvious reason why 1) higher proportions of one-series than ten-series tags were detached, or 2) higher proportions of ten-series than one-series tags were detached at the east Hudson site (Table 3), causing the significance in the ANOVA of the series and tagging location-series interaction (Table 2). If tilefish were contagiously distributed, one might expect these results from the ANOVA and also expect overall tag loss to be contagiously distributed along longlines. A runs test (Sokal and Rohlf 1969) failed to demonstrate contagion in tag loss, and Grimes et al. (1982a) failed to demonstrate contagion for longline catches using the same statistical procedure. The significantly greater tag loss at the west Hudson site (Tables 2, 3) presumably reflects greater tilefish abundance there.

Attachment strength was deemed significant by the ANOVA because increasing proportions of tags were lost with decreasing attachment strength (Table 3). Apparently tilefish were able to detach most easily those tags with 0.9 kg monofilament, followed by 1.8 and 2.7 kg. Among tags returned, four were attached with 1.8 kg and two with 2.7 kg monofilament (Table

TABLE 1.—Numbers of detachable tags of various hook types and attachment strengths set, detached, and returned at east and west Hudson Canyon tagging locations, August and September 1979.

Attachment strength (kg)	Hook type	Set		Detached		Returned	
		East	West	East	West	East	West
0.9	Straight	81	82	22	43	—	—
1.8		80	81	12	39	—	—
2.7		81	80	12	30	—	—
		242	243	46	112		
Total no.		485		158			
0.9	Circle	78	147	19	67	—	—
1.8		81	140	14	55	—	4
2.7		81	144	17	54	—	2
		240	431	50	176		6
Total no.		671		226			[1]7
Total no. tags set and detached		1,156		384			
Total no. tags set, detached and returned		482	574	96	288		

[1]Includes one hook of unknown attachment strength.

TABLE 2.—Analysis of variance of the proportions of tags detached at east and west Hudson Canyon locations, August and September 1979.

Source of variation	df	Sum of squares	Mean square	F value	P>F
Tagging location	1	0.2724	0.2724	61.53	<0.01
Series	1	0.0486	0.0486	10.98	0.01
Tagging location-series	1	0.1059	0.1059	23.91	<0.01
Attachment strength	2	0.0379	0.0190	4.28	0.05
Attachment strength-tagging location	2	0.0039	0.0019	0.44	0.66
Attachment strength-series	2	0.0016	0.0008	0.18	0.83
Hook type	1	0.0154	0.0154	3.47	0.10
Hook type-tagging location	1	0.0212	0.0212	4.80	0.06
Hook type-series	1	0.0002	0.0002	0.04	0.84
Hook type-attachment strength	2	0.0123	0.0062	1.39	0.30
Standard error	9	0.0399	0.0044		
Total	23	0.5593			

1). Evidently 0.9 kg monofilament attachment did not offer sufficient resistance for the hook to pierce the jaw and tag the fish. Furthermore, it did not take an exceptionally large fish to detach a tag because the returned tag with 2.7 kg monofilament was removed from a 3.2 kg fish.

Hook type and the hook type-tagging location interaction approached the 0.05 significance level as sources of variation in the ANOVA (Table 2) because higher proportions of straight hooks were detached, except for tagging longlines set at the east Hudson site where slightly higher proportions of circle hooks were lost (Table 3). These results suggest that fish are more easily hooked by straight hooks. However, all tags returned had circle hooks (Table 1); thus, although straight hooks tagged more fish, they apparently did not remain in the jaws as well.

The returned tags (7) represent about 2% of the maximum number theoretically deployed (384). However, because an unknown number of tags were observed to be lost due to fouling during setting and retrieval, the true rate of return is >2%. This return rate is comparable with that reported for marine tagging studies on relatively deep-dwelling reef fishes using conventional tags applied at the surface (Grimes et al. 1982b). Our tagging technique appears to be useful over relatively long periods. Tagged fish were at liberty from 115 d (0.32 yr) to 577 d (1.6 yr) (Table 4). Similarly, Phillip's (1968) only detachable tag return was from a marked kelp bass at liberty about 2 yr. All of our returns suggest that tilefish in the vicinity of Hudson Canyon are relatively sedentary, which might be expected given that tilefish inhabit (and presumably construct) extensive burrows (Able et al. 1982).

This tagging procedure may represent one of the few workable procedures presently available for investigating deep-dwelling fish. Optimal tag design could be determined by a preliminary study, as we have demonstrated (e.g., the optimal detachable tag for tilefish is constructed with a circle hook, serially numbered and addressed, and attached with 1.8 kg test monofilament). Studies using this procedure could be relatively inexpensive because the major expense in most marine fish-tagging studies—vessel time—would be eliminated. However, problems with the detachable tagging technique may make its use questionable for determining population parameters other than movement. As with other tagging procedures, mortality of tagged animals may be increased, especially since tags are placed in the mouth and could impair feeding. However, all recaptured animals in our study were reported in good condition with no obvious scars, wounds, or other signs of stress. Gut hooking (swallowed hooks) may also cause additional tagging mortality. In a longline assessment study (Grimes et al. 1982a) about 4% of all hooked fish seen (42) from a submersible were gut-hooked.

Unlike conventional tagging procedures, the researcher using detachable tags does not know what species (and their relative numbers) were marked, other than the target species. This was not a problem in our tilefish study because this fishery is virtually monospecific; if detachable tags are administered via a fishery, as in the case we described, tagging data can be adjusted according to the relative abundance of species in the catch.

It may also be possible to use detachable tags to estimate other population parameters, such as total mortality, if sufficient return data are available and assuming that tags are not lost from fish over the experimental period. For example, mortality could be estimated either from the ratio of numbers of tagged

TABLE 3.—Weighted mean proportions of tags detached according to hook type, tagging location, series (see Methods section) and attachment strength.

	Hook type		Tagging location		Series		Overall mean
	Straight	Circle	East	West	One	Ten	
Attachment strength (kg)							
0.9	0.40	0.32	0.24	0.47	0.39	0.32	0.36
1.8	0.32	0.24	0.16	0.39	0.33	0.23	0.28
2.7	0.26	0.27	0.18	0.36	0.32	0.22	0.27
Tagging location (all attachment strengths)							
East Hudson Canyon	0.19	0.20			0.17	0.22	0.19
West Hudson Canyon	0.46	0.35			0.52	0.30	0.41

TABLE 4.—Returns from tilefish tagged in the west Hudson Canyon, 1979. n.a. = not available.

Tag	No. days at liberty	Retrieval site	Fish weight and condition
1	115	tagging site	5.5 kg (good)
2	256	tagging site	n.a.
3	256	tagging site	n.a.
4	257	tagging site	n.a.
5	257	tagging site	n.a.
6	365	tagging site	2.3 kg
7	577	1.9 km west of tagging site	3.2 kg (good)

individuals to total individuals caught over time, or from the number of tagged individuals caught per unit of fishing effort over a specified period of time (Jones 1976).

In conclusion, we believe this procedure can be of value to fishery biologists desiring to investigate migration and movement (and perhaps mortality) of deep-dwelling fishes not markable by more conventional methods.

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We initiated our studies of tilefish and their fishery largely through the urgings of our friend the late Lionel A. Walford. The project could not have succeeded without the cooperation of longline fishermen from Barnegat Light, N.J. Captains John Larson and Ron Minor, owner and operator, respectively, of the longliner *Lori L*, kindly allowed us to set and retrieve tagging longlines. Captains Mike and Augie Ciell set and retrieved tagging longlines from FV *Panther*. Captains Keith Larson, Richard Moch, Curt Blensinger, and Bob McKnight returned recaptured tags. Valuable statistical advice was provided by Richard J. Trout, Rutgers University.

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Brown, Robin F., and Bruce R. Mate, "Abundance, movements, and feeding habits of harbor seals, *Phoco vitulina*, at Netarts and Tillamook Bays, Oregon," pages 291-301.

Page 294, first column, second line, correct line to read: (20.0%), by Everitt et al.[6]

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